

Translocating *Panicum virgatum* L.:
Performance, Community Impact and Competitive Outcome

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Dedication

To my spouse, Angela Putman, and my mother, Marcia Fairbanks, with love and deep gratitude.

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Dissertation Abstract

Recently, recognition of anthropogenic environmental impacts, the extent of human dependence on ecosystem services, and the benefits potentially conferred by the emerging bioeconomy, have greatly increased. Grassland reconstructions are one strategy for mitigating negative, and enhancing beneficial, human-environment interactions. Whether directly motivated by an interest in restoration or in bioenergy production, the process of reconstructing grasslands requires plant populations be translocated into sites from which they have previously been absent. Such translocations are associated with various risks.

The loci of these risks may be the translocated or neighboring wild populations, or the reconstruction site or adjacent areas. For example, insufficiently vigorous or inadequately adapted populations may fail to establish or persist; alternatively, strongly competitive populations can become overly dominant in reconstructed communities. In either case, biodiversity and function may be impaired and projects may fail to meet performance targets. Vigorous translocated populations may colonize areas outside the reconstruction site, either by vegetative spread, seed dispersal, or introgressive gene flow into neighboring wild populations. In the first two instances, translocated populations may become naturalized or even invasive; in the second two, the persistence and genetic diversity of wild populations may be compromised.

I investigated plant population performance, competitive outcomes, and recipient community impacts for switchgrass (*Panicum virgatum* L.), a species that is commonly incorporated into reconstructed grasslands. Because such efforts generally utilize seed produced in agronomic-scale increase fields, I focused my investigations on two salient characteristics: history of artificial selection and the number of foundation populations from which strains were derived. Artificially-selected cultivated varieties (cultivars) are expected to be more vigorous, competitive, and suppressive of community biodiversity than are strains that are not deliberately selected (ecotypes). Strains derived from multiple foundations are expected to be more genetically diverse than their single-foundation counterparts; if at least one foundation is adapted to site conditions, short-term establishment may balance the adaptive potential required for population persistence. Putatively greater diversity could manifest as moderate performance across multiple sites; in contrast, single-foundation strains may perform well at sites that resemble those at which they originated but poorly elsewhere.

This dissertation elucidates the effects that selection history and foundation-number have on switchgrass vigor and competitiveness, and plant community diversity and performance, so as

to help inform germplasm-sourcing decisions for grassland reconstructions. In Chapter 1, I examined the effects that selection history had on switchgrass stand density, persistence, and aboveground biomass, and tested whether multi-foundation strains performed consistently across four sites. Cultivar and ecotype biomass did not differ and while cultivars exceeded ecotypes in stand density, cultivar persistence was lower due to self-thinning. Strains' geographic origin was related positively to stand density and negatively to biomass across evaluation sites. I found no evidence, however, that multi-foundation strains performed more consistently across sites than did single-foundation strains. Collectively, these results suggest that cultivars may colonize adjacent areas through strong propagule pressure exerted by dense stands but colonization would not necessarily result in extreme dominance. Switchgrass establishment and persistence vary through the interaction of geographic origin and reconstruction location.

In Chapter 2, I measured the effects of switchgrass selection history and foundation-number on plant community diversity and switchgrass performance in experimental prairie plots that harbored cultivars or ecotypes. The effects of switchgrass characteristics on community abundances, biomass, species richness, diversity, and evenness were variable, generally small, and inconsistent among evaluation sites. Cultivars exceeded ecotypes in establishment, third-year stand density, and biomass but effects were modest and site-contingent. My results suggest that modestly stronger performance by cultivars does not translate into adverse effects on plant diversity. Under strong competition from weeds, switchgrass does not persist; adequate site preparation and management are necessary for successful switchgrass establishment. Switchgrass is unlikely to naturalize in reconstruction-adjacent areas that are heavily vegetated.

In Chapter 3, I evaluated competitive response and effect of juvenile switchgrass cultivars, ecotypes, and wild collections when grown with heterospecifics commonly found in reconstructed grasslands. Height and biomass were generally lowest in wild collections and similar for ecotypes and cultivars. However, belowground biomass in cultivars exceeded that of the other groups. All switchgrass groups were shortest, smallest, and allocated the most to aboveground tissues when grown with an annual forb. Cultivar biomass was greatest when grown with a perennial C3 grass. I found little evidence of variation among switchgrass groups in competitive effect; however, competitor belowground biomass was lowest when grown with cultivars. History of selection in switchgrass contributes to intraspecific differences in competitive outcomes and should be taken into account when sourcing germplasm for reconstructed grasslands.

Collectively, these chapters suggest that switchgrass is unlikely to become overly dominant within reconstructed grasslands or to pose an invasive threat to adjacent vegetative areas. Artificial selection has increased cultivar performance relative to ecotypes and wild collections but the differences are contingent on site conditions and competition regime. Discussion of the risks posed by translocated switchgrass populations should shift away from invasiveness and focus on the impacts of gene-flow between translocated and wild populations.

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Chapter 1:
Effects of source-population characteristics on
switchgrass (*Panicum virgatum* L.) performance in monoculture

Summary

The emergent bioeconomy offers substantial social, economic, and environmental benefits. These will be sharply reduced if harms associated with particular bioeconomy sectors are realized; one salient concern is the potential invasiveness of dedicated biofuel crops. Switchgrass (*Panicum virgatum* L.) is under development as a biofuel feedstock but the invasive potential of biofuel strains is unknown. Risk assessments may be informed by comparisons of extant strains that differ with respect to characteristics that could influence invasiveness. Two such characteristics are domestication history and adaptive genetic diversity. In a three-year field experiment, domesticated (cultivars) and non-domesticated (ecotypes) strains were compared with respect to performance. This experiment was also used to test whether strains derived from multiple foundation populations, being putatively more genetically varied, performed more consistently across four evaluation sites than single-foundation strains. Third-year biomass did not differ between cultivars and ecotypes. Cultivars exceeded ecotypes in stand density but had lower persistence due to self-thinning after the first year. No evidence was found for greater cross-site consistency in the performance of multi-foundation strains. Unanticipated trends were observed between switchgrass performance and geographic origin; stand density increased and biomass decreased along a southeast-to-northwest gradient in origin. Switchgrass cultivars may colonize adjacent areas through propagule pressure exerted by dense stands; however, similar levels of biomass between cultivars and ecotypes indicate that cultivars may not strongly dominate colonized ecosystems. Variation in performance within and among switchgrass strains is partially due to interactions between geographic origin and planting location.

Introduction

Joint interest in energy independence, food security, rural development, sustainability, and climate-change mitigation are stimulating an emergent bioeconomy (Pfau *et al.*, 2014; Chen & Zhang, 2015). Envisioned as the replacement of fossil fuel-based energy, materials, and chemicals by those derived from lignocellulose and other renewable resources, an advanced bioeconomy could confer substantial social and environmental benefits (McCormick & Kautto, 2013). However, particular bioeconomy sectors are associated with potential harms, including invasiveness of species grown as biofuel feedstocks (Kwit & Stewart, 2012; Pfau *et al.*, 2014).

One nascent biofuel crop is switchgrass (*Panicum virgatum* L.), a perennial grass native to most of the conterminous U.S. It is a promising source of lignocellulose due to its relative lack of insect pests (Webster *et al.*, 2010), long-lived stands, large potential yields, and high nutrient- and water-use efficiencies (Parrish & Fike, 2005). Dedicated biofuel strains of switchgrass are in active development (Wullschleger *et al.*, 2010; Vogel *et al.*, 2014). Switchgrass is productive on agriculturally marginal lands, which could decrease conflicts between food and biofuel production relative to other bioenergy crops (Sala *et al.*, 2009; Tilman *et al.*, 2009); also, the cultivation of switchgrass is expected to provide ecosystem services. These include carbon sequestration, soil stabilization, and wildlife habitat (McLaughlin & Walsh, 1998; Sanderson *et al.*, 2006; Blank *et al.*, 2014), although habitat value is reduced when switchgrass is grown in monoculture (Webster *et al.*, 2010; Hartman *et al.*, 2011; Blank *et al.*, 2014). Switchgrass establishes readily from seeds that are easier to harvest, clean, and sow than other candidate biofuel species (Gonzalez-Hernandez *et al.*, 2009).

Ecological risks associated with switchgrass cultivation include land-use change, biodiversity loss, and gene-flow impacts (Fletcher *et al.*, 2011; Hartman *et al.*, 2011; Kwit & Stewart, 2012; Blank *et al.*, 2014). Arguably the most salient is invasiveness (Barney & DiTomaso, 2010b; Davis *et al.*, 2010). Invasive species cause substantial economic and environmental costs (Pimental *et al.*, 2005); the net benefits accrued from renewable biofuels would be substantially reduced if biofuel crops became invasive (Davis *et al.*, 2010; US EPA, 2011). Traits associated with switchgrass and other native biofuel crops - C4 photosynthesis, tolerance of poor soils, vegetative reproduction, high stand density, high water-use efficiency, perennial growth habit, and pre-senescence translocation of nutrients - substantially overlap those observed in invasive plant species (Parrish & Fike, 2005; Raghu *et al.*, 2006; Sala *et al.*, 2009; US EPA, 2011). Although “invasive” is often defined as being non-native to the region in question (Executive Order 13112), hybridization of previously allopatric genotypes or substantial changes

in environmental context can render native species invasive (Saltonstall, 2002; Lavergne & Molofsky, 2007; Simberloff, 2008). Simberloff (2008) pointed out that large-scale cultivation of native species for biofuel will entail both hybridization and changes in context.

Cultivation and production practices could contribute to switchgrass invasion of non-cultivated areas. If deployed, biofuel switchgrass stands are expected to occupy substantial acreage (Groom *et al.*, 2008; Hartman *et al.*, 2011) and to be productive for 5-7 years or more before reseeding is required (Christensen & Koppenjan, 2010). Cultivation on these spatio-temporal scales increases the likelihood of escape from cultivation (Smith *et al.*, 2013) and imposes considerable propagule pressure on non-cultivated areas. Propagule pressure, which is strongly associated with both population invasiveness and ecosystem invasibility (Coalautti *et al.*, 2006), is likely to be increased unintentionally during feedstock production, harvest, and transport (Barney & DiTomaso, 2010b).

There is little evidence in the published literature of switchgrass escape from cultivation (Parrish & Fike, 2005; Kwit & Stewart, 2012) despite its use for forage, roadside stabilization, and ornamental purposes. However, weed risk assessments have found a high risk of switchgrass invasiveness outside its historic range - specifically, in irrigated and riparian areas of California and much of the western U.S. (Barney & DiTomaso, 2008, 2010a, 2011; DiTomaso *et al.*, 2013) as well as Hawai'i (Buddenhagen *et al.*, 2009). Extant, domesticated switchgrass strains that have been selected for vigor and nutrient-use efficiency may become weedy anywhere in the U.S. (US EPA, 2011). The development of dedicated biofuel switchgrass strains will entail intensive selective breeding by conventional, functional-genomic, and transgenic means (Sanderson *et al.*, 2006; Gressel, 2008; Wolt, 2009; Fu *et al.*, 2011; Kwit & Stewart, 2012; Shen *et al.*, 2013; Vogel *et al.*, 2014) and the potential invasiveness of such strains is unknown (US EPA, 2011). This potential, combined with invasive traits, strong propagule pressure, and unintentional seed dispersal, generates a non-trivial probability of switchgrass invasiveness (Barney & DiTomaso, 2010b; Kwit & Stewart, 2012).

Many have called for proactive risk assessments prior to the large-scale production of switchgrass and other second-generation biofuel crops (e.g., Barney & DiTomaso, 2010b; Chimera *et al.*, 2010; Davis *et al.*, 2010); however, such assessments are hampered by a lack of empirical data. Few biofuel switchgrass strains have progressed beyond experimental stages (but see Vogel *et al.*, 2014), so direct assessment of invasiveness in biofuel switchgrass is difficult. However, many domesticated strains of switchgrass have been released, and, like other native-grass cultivars, were selected for desirable agronomic traits that are associated with invasiveness

(e.g., Barker *et al.*, 1988; Boe & Ross, 1998). In contrast, non-domesticated switchgrass strains are considered to be noninvasive in their native range (US EPA, 2011). In the absence of biofuel strains, insight into potential switchgrass invasiveness may be gained by comparing agronomic cultivars to ecotypes - genetically distinct, non-domesticated populations that develop through adaptation to local conditions (Turesson, 1922; Hufford & Mazer, 2003).

The risk of switchgrass invasiveness is also influenced by genetic diversity; comparisons of putatively more- and less-diverse populations could inform cultivation practices and risk management. Both domesticated and non-domesticated switchgrass strains may be produced from a single foundation or from multiple populations. The deliberate combining of multiple foundation populations (“composite provenancing”) is one strategy for enhancing genetic variation in translocated populations (Broadhurst *et al.*, 2008; Weeks *et al.*, 2011) and for increasing survival, flowering, and fruiting rates in reintroduced plant populations (Godefroid *et al.*, 2011). If at least one foundation is adapted to local conditions, this approach can balance short-term establishment with the adaptive potential needed for population persistence (Rice & Emery, 2003; Kramer & Havens, 2009). However, populations that contain greater genetic variation are more likely to become invasive than are their less-varied counterparts (Anderson *et al.*, 2006b), as the former may be more likely to contain individuals capable of naturalizing in a particular environment (Stebbins, 1969) and of colonizing a wider range of environments (Ellstrand & Schierenbeck, 2000; Lavergne & Molofsky 2007). Putatively greater diversity, if adaptive, could manifest as moderate performance across multiple sites; in contrast, less-varied populations may perform strongly at sites resembling those of their origin (Hufford & Mazer, 2003) but weakly elsewhere.

There is a critical need to assess traits related to invasiveness in domesticated and non-domesticated strains of potential biofuel crops (Quinn *et al.*, 2010) but few such comparisons have been published. Casler *et al.* (2007b) reported switchgrass percent-cover and biomass values for two ecotypes that were within or below the range of values reported for four cultivars; however, the cultivar-ecotype differences were not specifically tested. A field experiment on five C4 grass species found that cultivars and ecotypes did not differ in aboveground biomass but all cultivars had modestly greater basal area than conspecific ecotypes (Wilsey 2010). Gustafson *et al.* (2004a) reported that two *Andropogon gerardii* cultivars exceeded a non-local ecotype in biomass and height but performed similarly to local ecotypes from remnant and restored prairies. A comparison of cultivars, non-local ecotypes, and naturalized invasive populations of *Phalaris*

arundinacea conducted in several environments found that cultivar biomass exceeded that of other groups only in upland, fertilized plots (Jakubowski *et al.*, 2011).

The goal of this experiment was to evaluate some aspects of invasive potential in switchgrass. Specifically, domesticated and non-domesticated switchgrass strains were compared with respect to traits associated with invasiveness and to examine the influence of genetic variation on these traits. Research objectives were to (1) compare the performance of cultivars and ecotypes in conditions mimicking likely biofuel crop production, i.e., monocultures (US EPA, 2011) and (2) assess whether putatively greater genetic variation is associated with consistent cross-site performance. It was hypothesized that cultivars would exceed ecotypes in stand density, persistence, and biomass and that multi-foundation strains would outperform single-foundation strains across sites.

Methods

Study species

Switchgrass (*Poaceae*) is monoecious, largely self-incompatible (Martinez-Reyna & Vogel 2002), and characteristic of tall- and mixed-grass prairies where it is generally sub-dominant to *A. gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium*. Switchgrass reproduces both rhizomatically and sexually; the flowering period extends from late June to early August and seed dispersal occurs from late August to early October (Sedivec *et al.*, 2009). Its minimum air-temperature tolerance is -42°C and it requires a minimum of 120 frost-free days for reproduction (USDA NRCS, 2015). Two ecotypes (*sensu lato*) have been identified (Porter, 1966). The upland type, which originates from more-northerly regions, can be tetraploid or octoploid, while the lowland type, which originates from southerly regions, is generally tetraploid (Barnett & Carver, 1967; Costich *et al.*, 2010; Zalapa *et al.*, 2011). Assignment to type was historically done morphologically (Parrish & Fike, 2005); more recently, assignment has been based on molecular methods (Zalapa *et al.*, 2011). Over a dozen switchgrass cultivars have been released (Zalapa *et al.*, 2011) and more are in development (e.g., Vogel *et al.*, 2014).

Experimental design

Common gardens were established in May-June 2010 at each of four sites in Minnesota (Morris, St. Paul, Staples, and Waseca; Fig 1-1, Table 1-1). Site histories varied: Waseca and Staples were previously in row-crop production; St. Paul had contained short-term agronomic research projects; Morris had been a pasture. No fertilizer was applied at Waseca, Staples, or St.

Paul for at least 6 – 8 months prior to plot installation. Morris received one application of manure from an organic dairy herd during that period. Site preparation followed recommendations for prairie restoration on ex-agricultural sites (Packard, 1997; Packard & Ross, 1997).

Twelve commercially-available switchgrass strains were used in this experiment (Table 1-2); all are plausible candidates for prairie restorations in Minnesota. Six strains were ecotypes and six were forage cultivars (Alderson & Sharp, 1995). ‘Dacotah’ is represented by two strains, each produced by a different grower (Table 1-2). There were seven single-, and five multi-foundation strains (Table 1-2). All the cultivars are upland-type (Moser & Vogel, 1995; Hultquist *et al.*, 1996), including ‘Cave-In-Rock’, which has been strongly established as such (Zalapa *et al.*, 2011) despite varying earlier descriptions (e.g., Tober *et al.*, 2007; Wullschleger *et al.*, 2010). All ecotypes used for this study were assumed to be upland types based on their geographic origins. Upon receipt, seeds were stored at room temperature (21°C) to reduce dormancy via after-ripening (Moser & Vogel, 1995). Prior to experiment installation, 28-day tests were conducted to obtain germination and viability rates. As all tested rates were within 10% of the values provided by the distributors, seeding-rate calculations were based on their data.

The 12 switchgrass strains were each sown into six randomly-assigned, 9 m² replicate plots per site. The seeding rate was 2 g m⁻² (17.5 lbs ac⁻¹), which is twice the rate recommended for establishing switchgrass as a bioenergy crop (Christensen & Koppenjan, 2010). This rate was intended to ensure adequate establishment despite anticipated competition from extensive weed seed banks. Seeds were not stratified prior to sowing.

Plots at Morris and St. Paul were mowed three times in 2010 to suppress annual weeds. Mowing was done under dry conditions with a flail mower when the weeds were 0.25-0.3 m tall, the cut height was approximately 0.15 m, and litter was removed manually with a hay-rake (Packard, 1997). In 2011, hand-clipping was required at the St. Paul site to remove *Cirsium arvense*, a state-listed noxious weed. Early in the 2012 growing season, litter and senesced material from the previous year were manually removed from all plots to ensure that subsequent biomass harvests collected only material produced in 2012.

Data collection and analysis

During the 2010, 2011, and 2012 growing seasons, censuses were conducted on all plants growing within a 0.25 m² quadrat in each plot. After the 2012 census, aboveground biomass was collected from a 1 m x 1 m area within each of 3 random plots per strain. Neither census data nor biomass samples were collected at Staples in 2012. The census quadrats and the biomass-

sampling areas were placed randomly within plots but at least 0.2 m from any plot edge; quadrat locations were rerandomized every year. Aboveground material was clipped at 4cm above the soil surface and sorted in the field as “switchgrass” or “weeds”. Samples were dried at 60 °C until no further loss of weight was observed; weights < 0.1 g were assigned a value of 0.05 g.

Switchgrass performance was characterized as annual stand density (individuals m⁻²), interannual change in stand density, stand persistence, and aboveground biomass. Change in stand density was calculated between the first and second, and between the second and third years. Persistence can be estimated as the change in stand density between specified time points (Beuselink *et al.*, 1984); in this study, it was calculated as (density_{year 3} - density_{year 1}) to account for delayed germination. Aboveground switchgrass biomass was measured in absolute terms and as a proportion of total aboveground biomass, where total biomass = switchgrass biomass + weed biomass. The effect of switchgrass source-population characteristics and strain on these performance measures was evaluated using univariate linear models (*R* v. 3.1.0, R Core Team, 2013). Models included main effects and all two-way interactions; higher order interactions were excluded because of associated difficulties in interpretation. Data were analyzed jointly across sites as well as for individual sites; in the former cases, “site” was included as a fixed effect. During analysis of the effect of switchgrass strain on performance, relationships between performance and geographic origin (latitude and longitude) became evident. The same approach was used to model these relationships. Intercept-only models were used to test whether interannual changes in stand density differed from zero.

For all models, residuals were visually assessed for compliance with parametric assumptions. In marginal cases, non-normality was tested with Shapiro-Wilk’s *W* and heteroscedasticity with Bartlett’s, Levene’s, or Fligner’s tests, as appropriate. Responses were transformed as necessary. Generally, count data were log- or square-root transformed, biomass data were square-root transformed, and proportion data were arcsine-square root transformed.

Results

Stand density

Analysis of all sites jointly indicated that cultivar stand densities were higher than ecotype densities for the first ($F_{1,275} = 77.5, p < 0.0001$), second ($F_{1,275} = 20.6, p < 0.0001$), and third years ($F_{1,275} = 19.4, p < 0.0001$) (Fig. 2). Other patterns, attributable to pairwise interactions of breeding history, foundation-number, and site, were variable. Notably, first-year stand density was highest for multi-foundation cultivars ($F_{1,275} = 7.20, p = 0.0078$), while third-year density

values were generally highest in multi-foundation cultivars but lowest in multi-foundation ecotypes ($F_{1, 206} = 13.5, p = 0.00030$, Fig. 2). Also, sites did not differ with respect to first-year stand densities ($p > 0.1$) but did for the second- ($F_{3, 275} = 28.3, p < 0.0001$) and third-year densities ($F_{2, 206} = 60.1, p < 0.0001$) (Fig. 1-2).

Joint-site analysis indicated that the 12 switchgrass strains differed significantly in stand density after the first ($F_{11, 240} = 13.8, p < 0.0001$), second ($F_{11, 240} = 3.96, p < 0.0001$), and third years ($F_{11, 180} = 5.55, p < 0.0001$); however, few patterns emerged. At each site, initial differences among strains decreased over time such that many strains had similar densities by the third year (Fig. 3). Site x strain interactions were significant for both second- ($F_{33, 2400} = 1.55, p = 0.034$) and third-year ($F_{22, 180} = 2.33, p = 0.0013$) stand densities (Fig. 3).

The relationship between geographic origin and stand density differed among years and evaluation sites (Table 1-3, Figs. 1-4, 1-5). Latitude and longitude of population origin were both positively related to stand density in all years ($p < 0.1$, Table 1-3); effects were strongest in the first year. Interactions between evaluation site and either longitude, latitude or both occurred during the second and third years but no consistent pattern emerged (Table 1-3).

Persistence

Analysis of all sites jointly indicated that stand densities declined both between the first and second ($F_{1, 287} = 73.1, p < 0.0001$) and between the second and third years ($F_{1, 215} = 5.08, p = 0.025$). The sharpest declines occurred during the first interval (Fig. 1-6). Persistence, expressed as change in stand density between the first and third years, was significantly lower in cultivars than ecotypes ($F_{1, 206} = 33.4, p < 0.0001$). Due to a marginally significant interaction between cultivar/ecotype identity and foundation-number ($F_{1, 206} = 3.25, p = 0.073$), persistence in multi-foundation ecotypes exceeded that of other groups.

Joint-site analysis indicated that populations differed with respect to the magnitude and direction of persistence ($F_{11, 180} = 5.83, p < 0.0001$); however, these trends were stable across sites ($p > 0.1$). ‘Summer’ and ‘Forestburg’ had the lowest persistence (greatest declines in density) whereas the LaCrosse ecotype exhibited the highest. *A posteriori* tests indicated that stand densities of most ecotypic populations, as well as ‘Cave-in-Rock’, declined less than did densities of the other cultivars (Fig. 1-7).

Biomass

Source-population characteristics had mixed effects on switchgrass aboveground biomass, as indicated by joint-site analyses. For example, and contrary to expectations, cultivar and ecotype biomass values did not differ significantly ($p > 0.1$) whether biomass was expressed

in absolute terms or as the switchgrass proportion of total aboveground biomass. However, absolute biomass was higher for single- than for multi-foundation strains ($F_{1, 98} = 7.09$, $p = 0.0091$) (Fig. 1-8A). Proportional biomass was lower for multi-foundation ecotypes than for any other group ($F_{1, 98} = 4.12$, $p = 0.045$) (Fig. 1-8B); a similar but non-significant trend ($p > 0.1$) occurred with absolute biomass.

In contrast to breeding history, geographic origin affected both absolute and proportional biomass (Table 1-3). Notably, a negative longitude x latitude interaction resulted in decreasing absolute biomass along a southeast-northwest gradient of geographic origins (Table 1-3, Fig. 1-9); a similar trend was observed for proportional biomass. Although values of absolute and proportional biomass differed among evaluation sites (Table 1-3), interactions between site and either latitude, longitude, or strain ($p > 0.1$) were not detected for either response. However, suggestive trends occurred at St. Paul, where southern strains produced approximately twice as much biomass as did northern strains, and at Waseca, where the largest differences appeared between the latitudinal end-members (Tables 1-1, 1-4).

Switchgrass biomass and switchgrass proportion of aboveground biomass differed significantly among sites ($p < 0.0001$) whether the covariates were source-population characteristics, geographic origin, or switchgrass strain (Figs. 1-8, 1-9; Table 1-4). Site mean values of absolute biomass ranged from 121 g m⁻² (1,000 lbs acre⁻¹) at Morris to 502 g m⁻² (4,400 lbs acre⁻¹) at Waseca.

Discussion

Switchgrass cultivars may be more likely than non-improved, putatively non-invasive ecotypes to colonize areas adjacent to reconstructions; however, confirmation would require additional data. The denser stands produced by cultivars provide a demographic advantage over ecotypes, assuming similar survival and reproduction in both groups. If fitness distributions are similar, higher stand densities would result in faster population growth rates for cultivars and potentially in greater propagule pressure on non-cultivated areas. Potentially higher introduction rates would not necessarily lead to extreme dominance in colonized habitats, however, as biomass values between cultivars and ecotypes were similar.

Alternatively, differences in seed dormancy or stand establishment among particular switchgrass strains could affect their relative potential for colonization or invasiveness. Because dormancy allows seedlings to partially escape crowding and sib competition (Venable & Brown, 1988; Rees, 1996), switchgrass strains with a large percentage of dormant seeds might have a

fitness advantage their low-dormancy counterparts. However, dormancy rates in switchgrass, which can be as high as 95% (Parrish & Fike, 2005), are difficult to predict because they vary substantially among strains, years, and nutrient levels (Mullen *et al.*, 1985; Vogel, 2002; Kimura *et al.*, 2015). Dormancy is thought to be high in non-domesticated switchgrass (Vogel, 2002); however, few published studies have directly assessed this (but see Mullen *et al.*, 1985). To the best of my knowledge, there is almost no published information on the extent to which cultivars and ecotypes categorically differ in this regard. Therefore, it is unclear whether the delayed germination exhibited by several ecotypes in this study represents a general trend.

There was no evidence of stronger across-site performance in multi- than in single-foundation strains. Conditions within and among sites or study years may have been too homogenous for genetic variation to confer an advantage. Further, for adaptation to result in differential performance, natural selection *in situ* would be necessary; this study was too short to encompass multiple generations. In fact, the multi-foundation strains may not have been more genetically variable. Because the genetic composition of any cultivated population results from intentional and unintentional selection exerted at different times, a strain derived from multiple narrowly-sampled populations may be no more varied than one developed from a single widely-sampled foundation. Alternatively, the multi-foundation strains may have been more genetically varied but maladapted. Given these possible explanations, these findings regarding foundation-number may not be generally applicable.

Sharp declines in stand density occurred between the first and second years, a pattern that is consistent with density-dependent mortality in the cultivars (self-thinning, Yoda *et al.*, 1963). This interpretation is supported by the high negative correlation between first-year stand density and initial change in stand density ($r = -0.87$). The density declines could also be due to winter mortality, as translocation distances in this study did exceed the 500 km maximum ($\sim 5^{\circ}$ latitude) recommended when moving switchgrass populations north (Moser & Vogel, 1995; Casler *et al.*, 2002; Casler *et al.*, 2007b). However, the first winter during the study period featured at least average monthly snowfall (Minnesota Climatology Working Group, 2014) that likely insulated switchgrass from monthly average temperatures that were slightly below the 30-year average. Additionally, and consistent with other studies (Jacobson *et al.*, 1984; Tober *et al.*, 2007), substantial mortality was observed in the putatively-adapted northern strains while southern-origin ‘Cave-In-Rock’ showed little decline.

The opposing trends in biomass and stand density as relation to latitude of origin are likely mediated by phenologic differences among switchgrass strains. Other studies have reported

latitudinal gradients in morphological characteristics and in phenology (*e.g.*, Boe, 2007; Tober *et al.*, 2007), with northern-origin strains having finer architecture and requiring fewer days to mature than southern-origin strains. This pattern, which may reflect adaptation to the length of growing season in strains' sites of origin and contribute to inter-strain variation in yield, is consistent with reported relationships between geographic origin and switchgrass performance (Jacobson *et al.*, 1984; Casler *et al.*, 2007b; Kaiser & Bruckerhoff, 2009; Jefferson & McCaughey, 2012).

The biomass values reported here are generally consistent with other work in Minnesota and South Dakota (*e.g.*, Jacobson *et al.*, 1984; Lee & Boe, 2005; Tober *et al.*, 2007). Contrary to some studies (Casler & Boe, 2003; Casler *et al.*, 2007b; Jefferson & McCaughey, 2012), no evidence of strain x site interactions for biomass was found in the current work. Published biomass values range widely, reflecting interactions between test-site location, geographic origin, phenology, and precipitation regime (Berdahl *et al.*, 2005, Casler, 2005, Parrish & Fike, 2005; Boe, 2007; Wullschleger *et al.*, 2010). For example, late-summer precipitation increases yields in 'Cave-In-Rock', which reaches anthesis in late August, but not 'Dacotah', which senesces in July (Tober *et al.*, 2007). All plots at a given site were harvested on the same date; variation among strains may thus have differed relative to yields obtained on separate dates but at similar phenologic stages.

As in the current work, other studies have reported substantial differences in switchgrass performance among evaluation sites (*e.g.*, Berdahl *et al.*, 2005; Tober *et al.*, 2007; Jefferson & McCaughey, 2012). Soil type, texture, and acidity are not considered to be strong drivers of such differences (Nixon & McMillan, 1964; Parrish & Fike, 2005; Wullschleger *et al.*, 2010). However, interactions between soil texture and precipitation can affect switchgrass emergence, establishment, and yield (Evers & Parsons, 2003; Wullschleger *et al.*, 2010) and these interactions may have affected performance in the current study. Another likely cause of differences among sites was competition from weeds, as indicated by the inverse of switchgrass proportions of total aboveground biomass.

There are several limitations to this work, two of which relate to conceptual scope. First, invasive potential was examined only in terms of stand establishment, persistence, and biomass. The substantial risks associated with propagule pressure and gene flow (Barney & DiTomaso, 2010a; Kwit & Stewart, 2012) were excluded from consideration. Second, no attempt was made to differentiate among cultivars on the basis of selection intensity. Researchers who distinguish between non-selected and selectively-bred switchgrass cultivars have asserted that non-selected

cultivars are essentially equivalent to natural populations, and that selectively-bred cultivars are representative of their foundation populations because few cycles of selection are imposed (*e.g.*, Casler *et al.*, 2007a; Zalapa *et al.*, 2011). According to this view, treating cultivars monolithically obscures pertinent variation. However, cultivars could not be meaningfully categorized for this study because selection intensity, which critically affects response to selection (Falconer & Mackay, 1996), is rarely quantified or documented in cultivar registration documents.

Additional limitations relate to duration and inherently variable data. All of the experimental stands used in this study were reproductively mature within two seasons; however, switchgrass stands may take three years or more to fully develop (Parrish & Fike, 2005). Additionally, switchgrass biomass varies substantially across years, sites, and strains (Lemus *et al.*, 2002; Lee & Boe 2005). A study that extended beyond three seasons or that included interannual biomass comparisons might reveal different patterns in performance. For example, continued recruitment within stands, or greater variability in interannual conditions, might have revealed differences between single- and multi-foundation strains in terms of across-site performance. This study did not encompass the winter of 2013-14, when extreme cold may have caused high mortality in southern-origin strains. Additionally, the choice of switchgrass populations was constrained. This resulted in small sample sizes within breeding-history and foundation-number groups and limited representation of any given geographic origin to two strains at most. Finally, strains may have been incorrectly assigned to their foundation-number categories, as this process depended on sometimes vague or conflicting information. Despite large overall sample sizes, these constraints and the variability inherent to this experiment limited the detection of differences.

A rigorous framework for assessing and managing the risks associated with large-scale cultivation of second-generation biofuels crops must be developed and implemented (Barney & DiTomaso, 2010b; Davis *et al.*, 2010; Hartman *et al.*, 2011; Smith *et al.*, 2013) but the window for proactively implementing such a framework is rapidly closing (Smith *et al.*, 2013). In its absence, various risk-mitigation practices could be adopted. The likelihood of stand failure could be reduced by translocating populations only within regions of adaptation that account for latitude and broad ecological conditions (Casler *et al.*, 2007b; Jefferson & McCaughey, 2012). The current study lends some support to this practice, as little evidence of strong differences in performance among strains originating across 9° of latitude and 12° of longitude was found. However, the large spatial scale of proposed adaptation regions poses additional concerns (Bischoff, 2014).

The risks of invasion (Davis *et al.*, 2010), gene-flow impacts (Kwit & Stewart, 2012) and pest or pathogen outbreaks associated with landscape-scale homogeneity (Hartman *et al.*, 2011) could be reduced by utilizing local ecotypes instead of (especially non-local) cultivars. Increased intra- and inter-population genetic diversity could confer some resistance to such outbreaks. Additionally, increased diversity could generate the adaptive potential that may be critical to population persistence under an increasingly variable climate (Jump & Peñuelas, 2005). Accordingly, remnant switchgrass populations should be protected, as these may be potential reservoirs of genetic diversity (Casler *et al.*, 2007a; Mutegi *et al.*, 2014). A complementary strategy involves investigating the potential for weediness at various stages of the development process and excluding germplasm that poses this risk from further domestication (Anderson *et al.*, 2006a). Finally, propagule pressure and invasive risk could be greatly reduced by the cultivation of sterile switchgrass (Barney & DiTomaso, 2008) but this may be practically difficult.

Conclusions

This study aimed to examine the potential invasiveness of switchgrass as a biofuel feedstock. Crops with low levels of domestication have naturalized outside of cultivation (Anderson *et al.*, 2006b). Switchgrass forage cultivars, which were found in this study to develop relatively dense stands, could colonize non-cultivated areas via strong propagule pressure. However, the biomass of forage cultivars was equivalent to that of switchgrass ecotypes, suggesting that colonization would not necessarily result in extreme dominance. Stand density and yield are both influenced by geographic origin, indicating that stand success will likely vary across strains and production sites. During this three-year experiment, no evidence was found for greater across-site performance by multi- than by single-foundation strains.

Current efforts to develop biofuel switchgrass involve the manipulation of extant cultivars, transgenic approaches, or both. However, these efforts should consider a broader suite of populations; the use of ecotypes for biofuel switchgrass could mitigate several ecological risks while not necessarily reducing yield. Bio-based fuels and the greater bioeconomy offer a number of ecological and social benefits but their value will be sharply reduced if biofuel crops such as switchgrass become invasive.

Tables

Table 1-1: Characteristics of four evaluation sites in Minnesota at which switchgrass cultivars and ecotypes, and single- and multi-foundation strains were compared with regards to performance.

Site	Latitude	Longitude	USDA		Soil family and subgroup
			plant hardiness zone	Soil series (type)	
Morris	45.59 ⁰ N	95.88 ⁰ W	4a	Doland (silt loam)	Fine-loamy mixed Udic Haploboroll
St. Paul	44.99 ⁰ N	93.17 ⁰ W	4b	Waukegan (silt loam)	Fine-silty over sandy or sandy-skeletal, mixed, superactive, mesic Typic Hapludolls
Staples	46.38 ⁰ N	94.81 ⁰ W	4a	Verndale (sandy loam) Oylen (sandy loam)	Coarse-loamy mixed Udic Argiborolls Coarse-loamy mixed Aquic Argiborolls
Waseca	44.08 ⁰ N	93.53 ⁰ W	4b	Webster (clay loam)	Fine-loamy, mixed, superactive, mesic Typic Endoaquolls

Table 1-2: Passport information for 12 commercial switchgrass strains. Distributors and producers are the same unless otherwise indicated. Latitudes and longitudes are estimates based on published accession data or producer records. Ploidy values: Zalapa *et al.*, 2011. Accession and release dates: Alderson & Sharp, 1995. Ecotypes' foundation-number values were provided by producers; some ecotype information is unknown or unavailable.

Strain	Producer / Distributor	Origin	Breeding history	Foundation number	Ploidy	Accession date(s)	Release date
Summer	SD Ag. Expmt. Station / Arvid Boe	Otoe Co., NE ^{2,3} 40.7°N, 95.9°W	Cultivar	One ^{5,7}	4x	1953	1963
Cave-in-Rock	Hamilton Native Outpost	Hardin Co., IL ¹ 37.5°N, 88.2°W	Cultivar	One ^{1,5}	8x	1958	1974
Dacotah 1	Kaste Seed /Ion Exchange	Morton Co., ND ⁴ 46.4°N, 100.9°W	Cultivar	One ⁷	4x	1935	1989
Dacotah 2	Carlson Prairie Seed /Ion Exchange	Morton Co., ND ⁴ 46.4°N, 100.9°W	Cultivar	One ⁷	4x	1935	1989
Sunburst	Kaste Seed	Union Co., SD 42.7°N, 96.6°W	Cultivar	Several ^{6,9}	8x		1983
Forestburg	Wind River Seed	Sanborn Co., SD 44.0°N, 98.1°W	Cultivar	Four ⁸	8x	1956, 1961	1983
Kossuth Co.	Shooting Star Native Seeds	Kossuth Co., IA 43.4°N, 94.2°W	Ecotype	One			
LaCrosse Co.	Shooting Star Native Seeds	LaCrosse Co., WI 43.9°N, 91.1°W	Ecotype	One			
Isanti 1	Taylor Creek Nursery	Isanti Co., MN 45.5°N, 93.3°W	Ecotype	One			
Iowa	Allendan	Multiple counties, IA 42°N, 93°W	Ecotype	Several			
Isanti 2	Prairie Restorations	Isanti Co., MN 45.5°N, 93.3°W	Ecotype	Several			
Clay Co.	Prairie Restorations	Clay Co, MN 46.9°N, 96.5°W	Ecotype	Several			

¹Hopkins *et al.*, 1995. ²Hultquist *et al.*, 1996. ³Boe, 2007. ⁴Barker *et al.*, 1990. ⁵Alderson & Sharp, 1995. ⁶Boe & Ross, 1998. ⁷Tober *et al.*, 2007. ⁸Barker *et al.*, 1988. ⁹Casler *et al.*, 2007b.

Table 1-3: Results from models of switchgrass performance as influenced by evaluation site, geographic origin, and 2-way interactions. Stand densities and absolute biomass were square-root transformed and proportional biomass was arcsine-square root transformed. Effect estimates are not back-transformed. Bold text indicates $p < 0.5$; bold italicized text indicates $p < 0.1$.

Response (adjusted r^2)	Fixed effects	Estimate	Std. error	F (df)	p		
Stand density 1 st -year (0.23)	Site			1.53 (3,275)	0.21		
		Morris (intercept)	-139	44.7			
		Staples	4.25	7.62			
		St. Paul	2.86	7.62			
		Waseca	7.49	7.62			
		Longitude	1.64	0.498	55.1 (1,275)	< 0.0001	
		Latitude	2.47	0.998	3.30 (1,275)	0.0011	
		Site x longitude			0.372 (3,275)	0.77	
			Staples	0.0728	0.117		
			St. Paul	0.0338	0.117		
			Waseca	0.0542	0.117		
		Site x latitude			1.05 (3,275)	0.37	
			Staples	-0.246	0.179		
			St. Paul	-0.126	0.179		
			Waseca	-0.286	0.179		
	Longitude x latitude	-0.0292	0.0110	7.13 (1,275)	0.0080		
2 nd -year (0.29)	Site			29.0 (3,275)	< 0.0001		
		Morris (intercept)	-38.6	28.4			
		Staples	-1.17	4.85			
		St. Paul	-6.14	4.85			
		Waseca	-0.992	4.85			
		Longitude	0.499	0.317	22.2 (1,275)	<0.0001	
		Latitude	0.684	0.635	4.14 (1,275)	0.043	
		Site x longitude			4.09 (3,275)	0.0073	
			Staples	-0.0719	0.0741		
			St. Paul	0.171	0.0741		
			Waseca	-0.0253	0.0741		
		Site x latitude			4.70 (3,275)	0.0032	
			Staples	0.217	0.114		
			St. Paul	-0.197	0.114		
			Waseca	0.0915	0.114		
	Longitude x latitude	-0.00878	0.00696	1.59 (1,275)	0.21		
3 rd -year (0.40)	Site			57.2 (2,275)	< 0.0001		
		Morris (intercept)	-62.2	22.2			
		St. Paul	-1.65	3.28			
		Waseca	0.651	3.28			
		Longitude	0.812	0.246	16.9 (1,275)	< 0.0001	
		Latitude	1.15	0.495	9.30 (1,275)	0.0026	
		Site x longitude			2.46 (2,275)	0.088	
			St. Paul	-0.0340	0.0501		
			Waseca	-0.109	0.0501		

	Site x latitude			4.55 (2,275)	0.012
		St. Paul	0.143	0.077	
		Waseca	0.230	0.077	
	Longitude x latitude		-0.0152	0.00544	7.80 (1,275)
<hr/>					
Biomass					
Absolute (0.60)	Site			48.3 (2,98)	< 0.0001
		Morris (intercept)	-558	220	
		St. Paul	38.7	32.5	
		Waseca	104	32.5	
	Longitude		7.13	2.44258	3.65 (1,98)
	Latitude		11.0	4.90	39.4 (1,98)
	Site x longitude				1.28 (2,98)
		St. Paul	-0.354	0.497	
		Waseca	-0.794	0.497	
	Site x latitude				0.175 (2,98)
		St. Paul	0.0727	0.762	
		Waseca	-0.349	0.762	
	Longitude x latitude		-0.142	0.0539	6.92 (1,98)
<hr/>					
Proportional biomass					
(0.69)	Site			96.0 (2,98)	< 0.0001
		Morris (intercept)	-35.6	10.6	
		St. Paul	2.11	1.571	
		Waseca	3.02	1.57	
	Longitude		0.436	0.118	5.24 (1,98)
	Latitude		0.730	0.237	32.9 (1,98)
	Site x longitude				0.418 (2,98)
		St. Paul	-0.0101	0.0241	
		Waseca	-0.0220	0.0241	
	Site x latitude				0.0615 (2,98)
		St. Paul	-0.0121	0.0369	
		Waseca	-0.00197	0.0369	
	Longitude x latitude		-0.00898	0.00261	11.8 (1,98)
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Table 1-4: Back-transformed, model-predicted means (\pm SE) of third-year aboveground biomass and proportion of total aboveground biomass for 12 commercially-produced switchgrass strains, analyzed jointly across 3 sites in Minnesota, USA. Biomass was square-root transformed. Proportional biomass was arcsine-square root transformed. Strains that share at least one bolded letter do not differ based on Student-Newman-Keuls a posteriori tests.

	BIOMASS				PROPORTIONAL BIOMASS			
	Morris	St. Paul	Waseca		Morris	St. Paul	Waseca	
Cave-in-Rock	221 (100, 81)	444 (138, 119)	1100 (211, 193)	a	0.38 (0.15, 0.14)	0.88 (0.08, 0.11)	0.98 (0.01, 0.06)	a
Summer	275 (110, 92)	446 (138, 119)	706 (171, 153)	ab	0.42 (0.15, 0.14)	0.86 (0.09, 0.12)	0.99 (0.01, 0.06)	a
Dacotah 1	73 (61, 42)	203 (96, 78)	210 (98, 79)	cde	0.14 (0.12, 0.09)	0.69 (0.13, 0.15)	0.62 (0.14, 0.15)	abc
Dacotah 2	25 (40, 21)	167 (88, 70)	220 (100, 81)	de	0.04 (0.08, 0.04)	0.48 (0.15, 0.15)	0.77 (0.11, 0.14)	bc
Sunburst	87 (66, 48)	402 (131, 113)	708 (172, 153)	abc	0.15 (0.12, 0.09)	0.91 (0.07, 0.10)	1.0 (0.01, 0.03)	a
Forestburg	86 (66, 47)	179 (91, 72)	214 (99, 80)	cde	0.19 (0.13, 0.10)	0.51 (0.15, 0.15)	0.77 (0.11, 0.14)	abc
Kossuth Co.	139 (81, 63)	410 (133, 114)	857 (188, 169)	ab	0.22 (0.14, 0.11)	0.87 (0.08, 0.12)	1.0 (0.002, 0.04)	a
LaCrosse Co.	46 (51, 32)	401 (131, 113)	551 (152, 134)	abcd	0.086 (0.10, 0.06)	0.88 (0.08, 0.11)	0.90 (0.07, 0.10)	ab
Isanti 1	15 (33, 14)	132 (79, 61)	464 (141, 122)	cde	0.030 (0.07, 0.03)	0.52 (0.15, 0.15)	0.93 (0.05, 0.09)	abc
Iowa	35 (45, 27)	436 (137, 118)	403 (132, 113)	bcd	0.071 (0.10, 0.06)	0.86 (0.09, 0.12)	0.92 (0.06, 0.10)	ab
Isanti 2	17 (35, 16)	121 (76, 58)	308 (116, 98)	de	0.038 (0.08, 0.04)	0.36 (0.15, 0.14)	0.73 (0.12, 0.14)	bc
Clay Co.	11 (29, 11)	74 (52, 43)	71 (61, 42)	e	0.019 (0.06, 0.02)	0.27 (0.14, 0.12)	0.32 (0.15, 0.13)	c

Figures

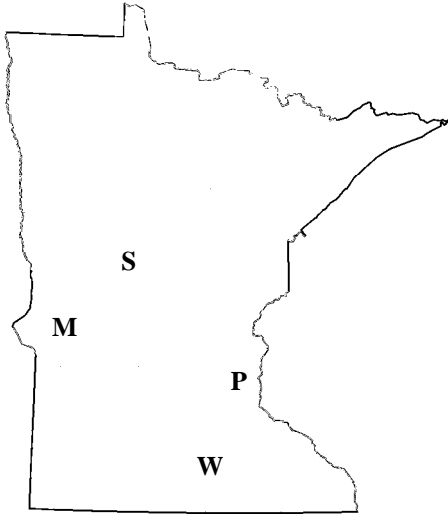


Fig. 1-1: Locations of four evaluation sites at which switchgrass cultivars and ecotypes, and single- and multi-foundation strains were compared with regards to performance; Minnesota, USA. M: Morris. S: Staples. P: St. Paul. W: Waseca.

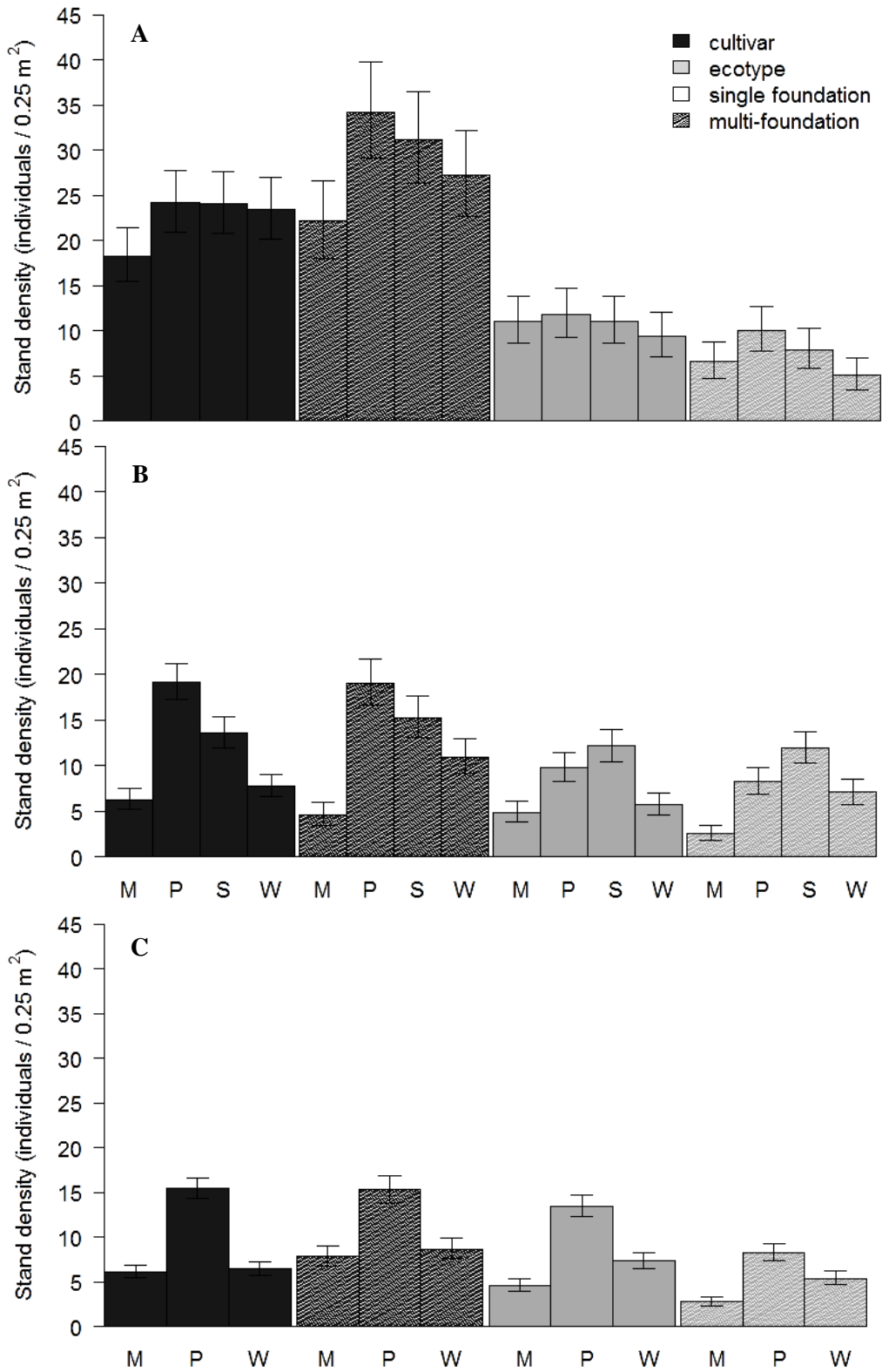


Fig. 1-2: Back-transformed (square-root) model-predicted mean switchgrass stand densities (\pm SE) evaluated across multiple sites in Minnesota, 2010-2012. Open bars: single-foundation. Hatched bars: multi-foundation. Not all data are available for all sites. A) 1st yr. B) 2nd yr. C) 3rd yr. M: Morris. P: St. Paul. S: Staples. W: Waseca.

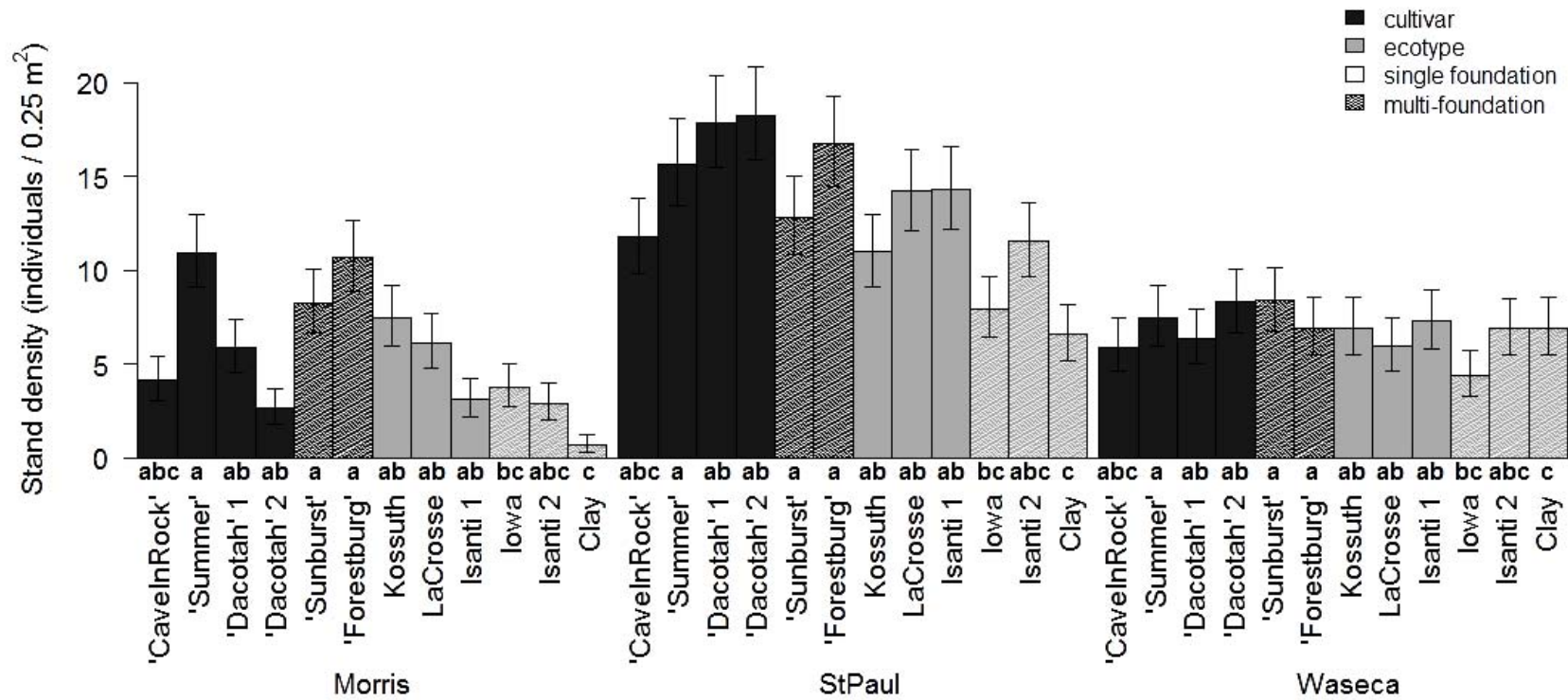


Fig 1-3: Back-transformed (square-root), model-predicted third-year stand densities (mean \pm SE) for 12 commercially-produced switchgrass strains evaluated across 3 sites in Minnesota. Open bars: single-foundation. Hatched bars: multi-foundation. Strains that share any bolded lower-case letters do not differ based on Student-Newman-Keuls a posteriori tests

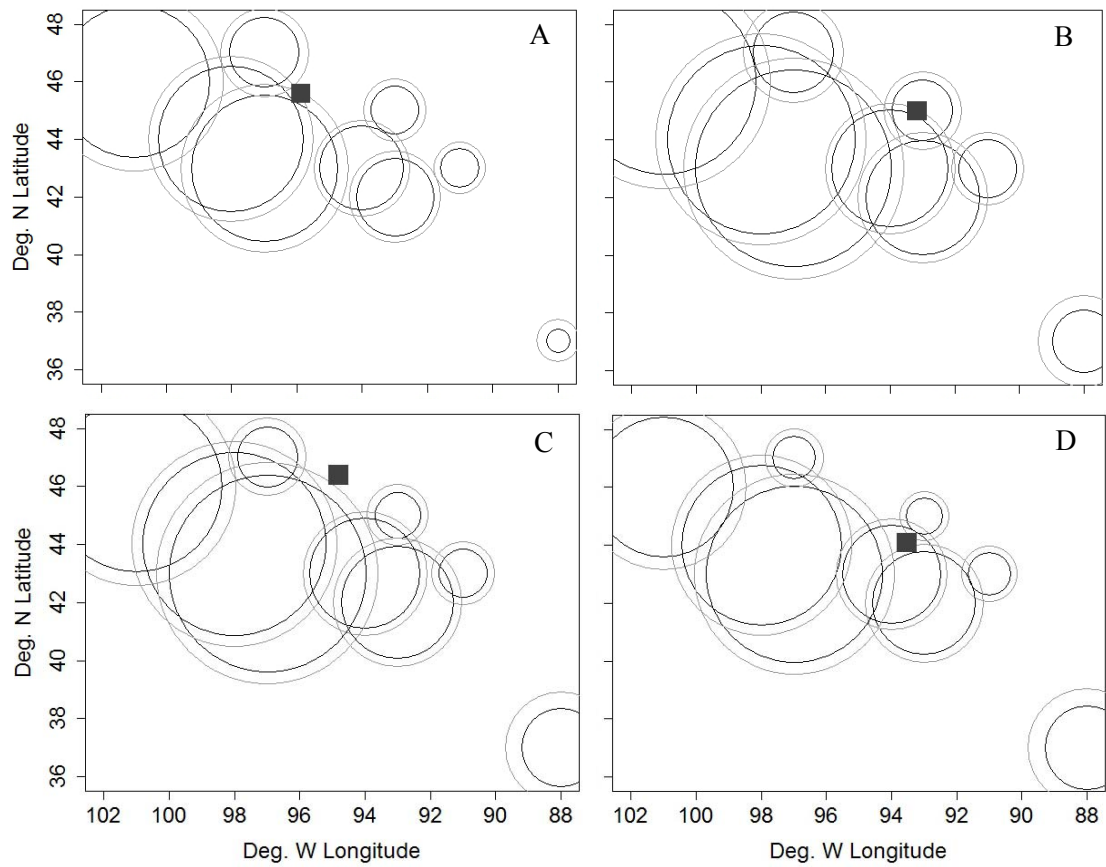


Fig. 1-4: Relative magnitudes of back-transformed (square-root), model-predicted, first-year stand densities (individuals 0.25 m^{-2}) for 12 switchgrass populations evaluated at 4 sites in Minnesota, USA: A) Morris. B) St. Paul. C) Staples. D) Waseca. Bubble centers indicate populations' sites of origin. Squares denote location of evaluation sites. Light gray circles denote $\pm 1 \text{ s.e.}$ Lower right: southeast. Upper left: northwest.

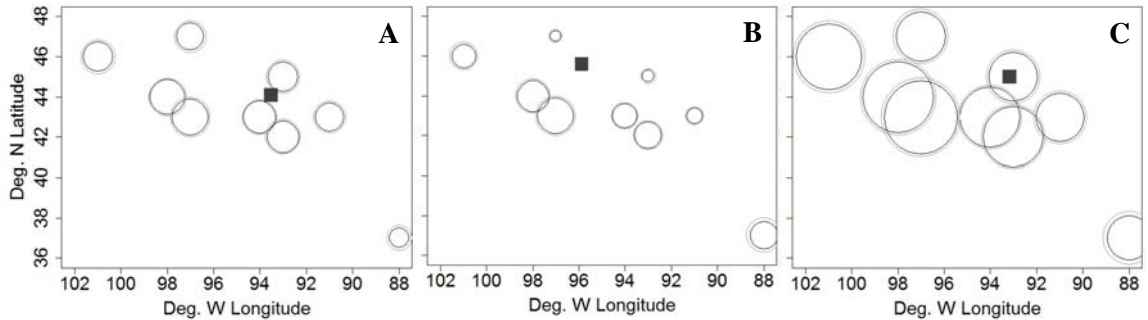


Fig 1-5: Relative magnitudes of back-transformed (square-root), model-predicted, third-year stand densities (individuals 0.25 m^{-2}) for 12 switchgrass populations evaluated at 3 sites in Minnesota, USA: A) Morris. B) St. Paul. C) Waseca. Bubble centers indicate populations' sites of origin. Squares denote location of evaluation sites. Light gray circles denote $\pm 1 \text{ s.e.}$ Lower right: southeast. Upper left: northwest.

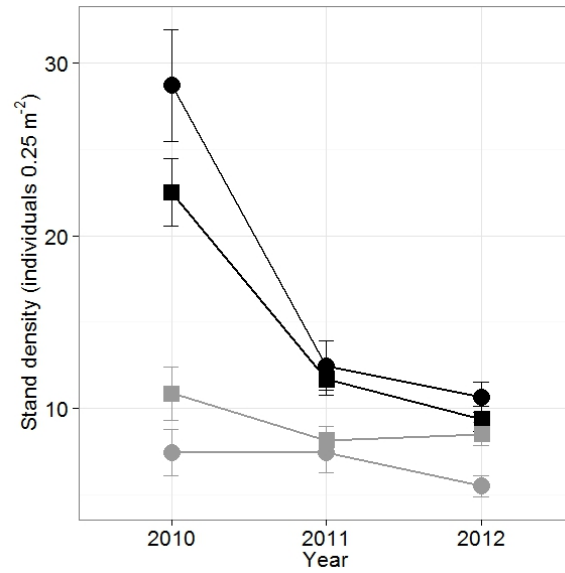


Fig. 1-6: Back-transformed (square-root), model-predicted mean switchgrass stand densities (\pm SE) evaluated at 4 (2010, 2011) or 3 (2012) sites in Minnesota, USA. Black: cultivars. Gray: ecotypes. Circles: single-foundation strains. Squares: multi-foundation strains.

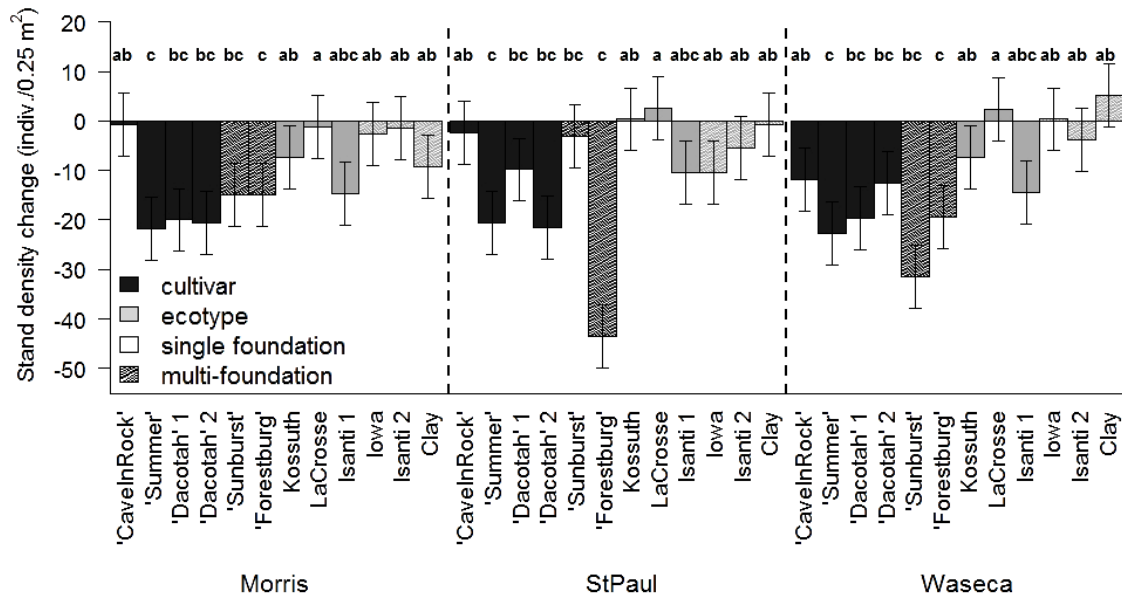


Fig. 1-7: Back-transformed (square-root), model-predicted switchgrass persistence (3^{rd} yr - 1^{st} yr stand density), jointly analyzed across 3 sites, Minnesota USA. Open bars: single-foundation. Hatched bars: multi-foundation. Strains that share any bolded lower-case letters do not differ based on Student-Newman-Keuls a posteriori tests.

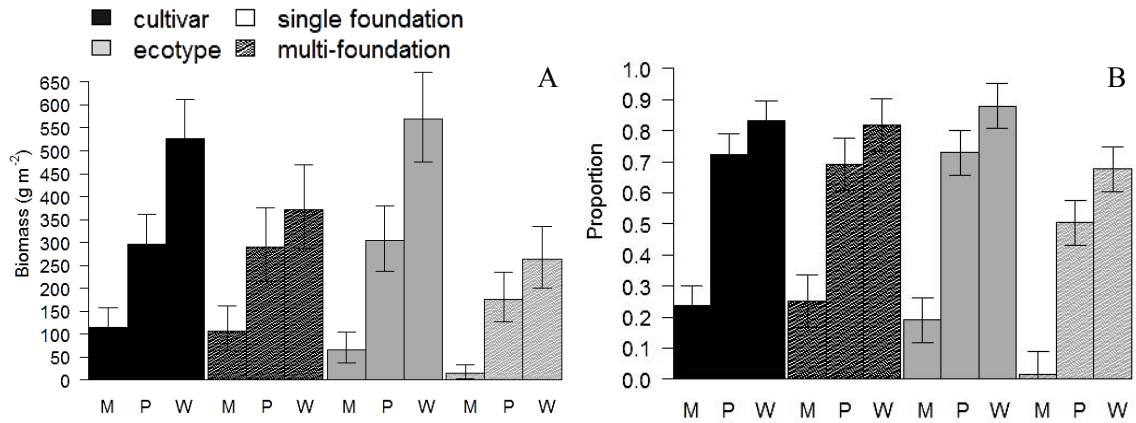


Fig. 1-8: Model-predicted third-year switchgrass yield jointly analyzed across 3 sites in Minnesota, USA. A) Biomass. B) Proportion of total aboveground biomass. Open bars: single-foundation. Hatched bars: multi-foundation. M: Morris. P: St. Paul. W: Waseca.

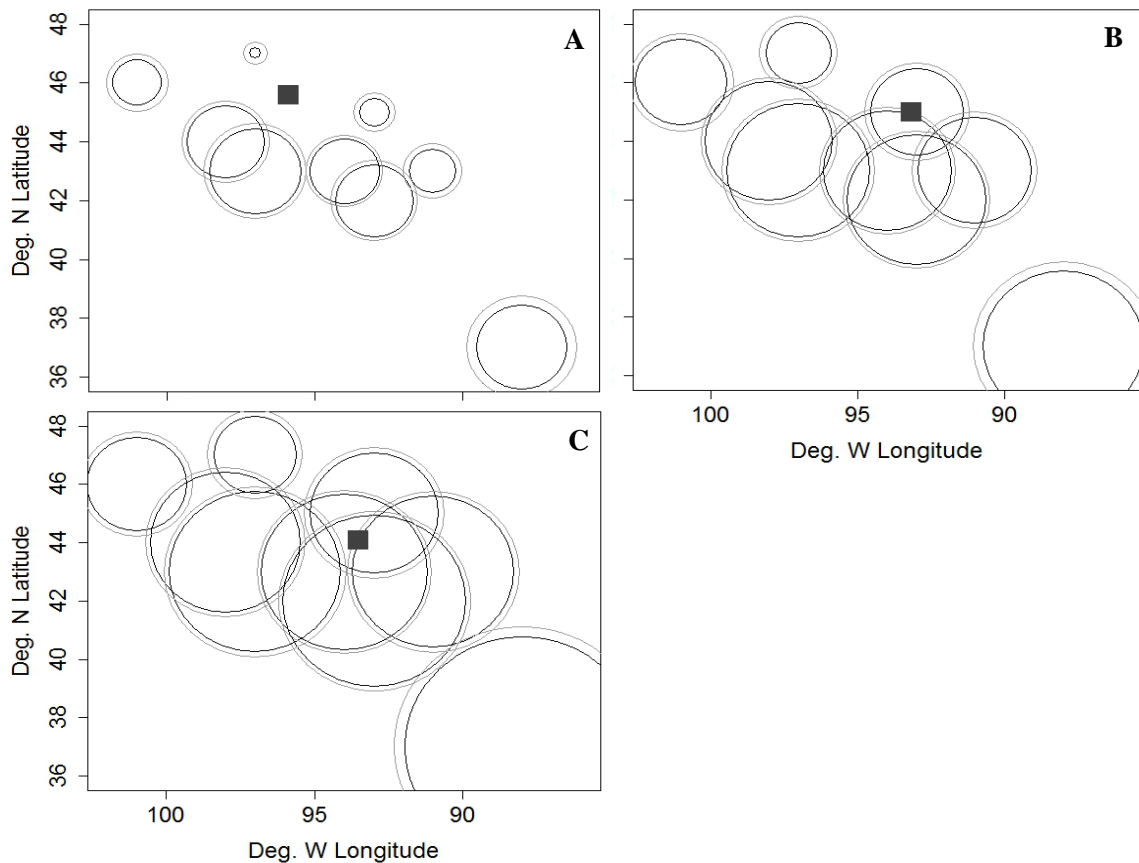


Fig. 1-9: Relative magnitudes of back-transformed (square-root), model-predicted 3rd-year aboveground biomass for 12 switchgrass populations evaluated at 3 sites in Minnesota: A) Morris. B) St. Paul. C) Waseca. Bubble centers indicate populations' sites of origin. Squares denote location of evaluation sites. Light gray circles denote ± 1 s.e. Lower right: southeast. Upper left: northwest.

Chapter 2:
Performance and diversity effects of translocated switchgrass
(*Panicum virgatum* L.) populations in experimental prairie communities

Summary

Ecological restoration and reconstruction of bioenergy grasslands are responses to environmental degradation that may differ in aim but similarly entail the translocation of native plant populations. These efforts entail various risks: translocated populations may fail to establish or they may overly dominate a recipient community; they must be adequately adapted to initial site conditions but have the potential to adapt to rapid environmental change. Breeding history, and the number of foundations combined during germplasm development, may affect these translocation risks. During a three-year field experiment, domesticated (cultivar) and non-domesticated (ecotype) strains of switchgrass, derived from either a single or from multiple foundation populations, were compared with regards to recipient communities and switchgrass performance. There was little evidence that breeding history or foundation number influenced measures of community performance and diversity; observed effects were generally small and variable among evaluation sites. Switchgrass cultivars exceeded ecotypes with respect to stand establishment, third-year stand density, and biomass; however, effect sizes were small and site-contingent. These results suggest that, at low seeding densities, modestly stronger performance by cultivars does not translate into adverse effects on plant diversity in establishing prairies. Switchgrass does not establish well or persist under heavy competition from weeds; adequate site preparation and management are necessary for successful switchgrass establishment.

Introduction

Two increasingly important responses to environmental degradation are ecological restoration (Hobbs & Cramer, 2008) and reconstruction of native grasslands for bioenergy production (Sanderson & Adler, 2008). The main goals of these two interventions differ. Ecological restoration, though difficult to define precisely (Higgs, 1997), aims to improve damaged lands and restore ecological potential (Bradshaw & Chadwick, 1980); bioenergy grasslands emphasize the production of aboveground biomass. However, both interventions are intended to enhance ecosystem services including wildlife and pollinator habitat, water purification, carbon sequestration, and aesthetic value; the fulfillment of these varied goals critically depends on the development of a diverse, resilient plant community (Tilman *et al.*, 2006; Fargione *et al.*, 2009; Blank *et al.*, 2014; Werling *et al.*, 2014).

Because native seed banks are commonly depleted due to previous land-use or management, achieving this diversity generally requires translocating plant germplasm (Menges, 2008). Translocation, which is the deliberate moving of a population from its site of origin to the reconstruction/restoration site, can introduce risks to the recipient community as well as to the surrounding landscape. Risks include the failure of translocated populations to establish or persist; extreme dominance of the restored/reconstructed community by highly fit translocated populations; and negative impacts of gene flow between translocated and neighboring remnant populations (Zavaleta & Hulvey, 2004; Baer *et al.*, 2005; McKay *et al.*, 2005; Vander Mijnsbrugge *et al.*, 2010). The nature and severity of these risks vary with site conditions, characteristics of the translocated population, and the proximity of remnant populations.

The actual occurrence of these problems can reduce the capacity of the restored/reconstructed community to meet project goals or can contribute to the loss of remnant populations. For example, the failure of a translocated population to establish or persist directly reduces diversity; in addition, delayed or weak establishment can facilitate colonization by exotic species (Zavaleta & Hulvey, 2004) that are associated with reduced native-species biodiversity (Vilà *et al.*, 2011). Over-dominance by one species can reduce community diversity (Baer *et al.*, 2005), decrease site-level resilience (Peterson *et al.*, 1998), and compromise the community's developmental trajectory (D'Antonio & Meyerson, 2002; Polley *et al.*, 2005).

Gene flow between translocated and remnant populations may reduce the fitness of either population through genetic swamping (Kramer & Havens, 2009) or outbreeding depression (Edmands, 2007), although arguably the consequences for remnant populations are more severe.

Reduced fitness is likely to be transient if both populations are well adapted to their environmental conditions, which are similar, and if the relevant genes recombine freely (McKay *et al.*, 2005). Gene flow may also contribute to positive restoration outcomes by alleviating inbreeding depression in small, isolated remnants (Richards, 2000; Edmands, 2007) or mitigating the decrease in genetic variation that frequently occurs in bottlenecked founding populations (Dlugosch & Parker, 2008). However, hybridization between previously allopatric populations has been implicated in the evolution of invasive traits (Lavergne & Molofsky, 2007; Schierenbeck & Ellstrand, 2009; Meyerson *et al.*, 2012).

When sourcing germplasm for translocation, restorationists must balance trade-offs among risks and consider adaptation to the local environment, evolutionary potential, population fitness, and germplasm availability, within the context of a landscape that may host both translocated and remnant populations. Local ecotypes (*sensu* Turesson 1922) are generally the preferred source for translocated populations. Ecotypes are presumed to be adapted to local conditions, be genetically similar to wild populations in their respective areas of origin, and pose a relatively low risk of negative gene-flow impacts on remnant populations (Hufford & Mazer, 2003; McKay *et al.*, 2005). However, local ecotypes have been characterized as having uneven establishment (Knapp & Rice, 1994) and ecotype seed is often insufficiently available (Tischew *et al.*, 2011).

Cultivated varieties (cultivars) are a potential alternative to ecotypes. Cultivars are commonly described as products of deliberate selection that consistently express high values of particular traits when grown under conditions to which they are adapted (Lesica & Allendorf, 1999; Aubry *et al.*, 2005). However, some plant breeders contend that selective breeding is not prerequisite for cultivar release (Casler *et al.*, 2007a; Zalapa *et al.*, 2011) and that even in cases of deliberate selection, insufficient generations have elapsed since accession to generate substantial divergence between a given cultivar and its source population (Casler *et al.*, 2007a). Debate notwithstanding, many native grass cultivars were developed as agronomic crops and were selectively bred to express high yield and growth rates and improved survival (Parrish & Fike 2005; Jakubowski *et al.*, 2011). These traits are shared by some invasive species (Raghu *et al.*, 2006), suggesting that grass cultivars could overly dominate restoration/reconstruction sites. Additionally, cultivars are often derived from small numbers of accessions (Alderson & Sharp, 1995) that are unlikely to be genetically representative of source populations. The extent to which cultivar use in restorations is appropriate and how best to balance the risk of ecotype under-establishment against that of cultivar over-establishment, are subjects of continuing disagreement

(Lesica & Allendorf, 1999; Burton & Burton, 2002; Booth & Vogel, 2006; Brown *et al.*, 2008; Wilsey, 2010).

Balancing the risk of maladaptation to initial site conditions with that of inadequate adaptive potential has also proven challenging. Reducing the risk of maladaptation by using locally-sourced materials has been recommended in the restoration literature and become best practice for some government agencies (e.g., Rogers & Montalvo, 2004; Vander Mijnsbrugge *et al.*, 2010). However, definitions of “local” vary, cases of higher fitness in non-local than in local populations have been documented (e.g., Hereford & Winn, 2008), and natural selection does not necessarily produce adaptively optimal phenotypes (Crespi, 2000). Levels of neutral genetic variation are often considered to reflect adaptive potential and have been estimated for some plant species (e.g., Gustafson *et al.*, 2004b; Moncada *et al.*, 2007; Zalapa *et al.*, 2011; Mutegi *et al.*, 2014). However, such studies are generally uninformative regarding quantitative-genetic traits (Reed & Frankham, 2001), which are the most salient to native-species translocations.

In the absence of data on quantitative-genetic variation in translocated populations, a proxy for genetic variability could assist sourcing decisions. The number of foundation populations from which a given material was derived may be such a proxy. Natural populations are known to harbor considerable quantitative-genetic variation (Hill, 2010), assuming adequate size to minimize genetic drift (Schaal & Leverich, 2005). Further, many natural populations are substantially differentiated with respect to the genes that underlie ecologically relevant traits (Linhart & Grant, 1996; Latta, 2003). If accessions well represent the genetic variation within and among wild populations and if genetic variation is maintained during plant-material development, then the variation in a strain derived from those accessions should increase with the number of foundation populations. Although sometimes imprecise or uncertain, foundation-number data are available for some commercial strains. Research is needed to ascertain the extent to which this characteristic affects the performance and community-impact of translocated populations.

The risks associated with translocating native species are particularly salient for switchgrass (*Panicum virgatum* L.) (Barney & DiTomaso, 2010b). This C4 species, native to North America, is an important component of prairie restorations and cultivars have been widely planted for forage and soil stabilization (Casler *et al.*, 2007b). Conventional and transgenic strains are under development as biofuel feedstock (Kwit & Stewart, 2012) and switchgrass is commonly included in bioenergy grasslands. The prospect of expanded switchgrass cultivation lends increased urgency to investigations of factors that contribute to its under- or over-establishment in recipient communities and to its potential for adaptation to future site conditions. Despite forecast

increases in native biofuel crops, few studies have examined the risks associated with large-scale translocations of native species including switchgrass (Barney & DiTomaso, 2008; Kwit & Stewart, 2012).

The goal of this research was to investigate risks associated with translocating switchgrass into establishing prairies by examining the occurrence of switchgrass under- or over-establishment, the impact on prairie plant communities of factors associated with differential establishment, and the utility of foundation-number as a predictor of degree of adaptation and potential for future adaptation. Specific objectives were to (1) compare diversity and performance between communities harboring switchgrass cultivars versus ecotypes; (2) evaluate the extent to which switchgrass performance in establishing communities differs between cultivars and ecotypes, and between single- and multi-foundation strains; and (3) investigate whether foundation-number predicts performance across sites. Cultivars were expected to be associated with lower community diversity and community biomass but with higher switchgrass performance than ecotypes; multi-foundation strains were expected to exhibit higher across-site performance than single-foundation strains.

Methods

Experimental design

The same species, sites (Fig. 1-1, Table 1-1), and strains (Table 1-2) were used for this experiment as for the work detailed in Chapter 1. At each site, 72 1 m² plots were installed and sown with a mix of prairie grasses (Table 2-1). Each of the 12 switchgrass strains was then sown into 6 randomly-assigned replicate plots per site and the soil was lightly raked to enhance seed-soil contact. A mix of prairie forbs and legumes was then oversown into all plots (Table 2-1). The grass mix was seeded at 1.06 g m⁻² of pure live seed (PLS), the forb mix at 0.28 g PLS m⁻², and switchgrass at 0.056 g PLS m⁻². These rates were based on a native-grass seed-drilling density of 11 kg ha⁻¹ (Kilde, 2000; McDonagh & Hallyn, 2010) and a 4:1 grass:forb seeding ratio. Grass- and forb-mix densities were calculated using germination and viability data provided by the seed producer (Prairie Restorations, Princeton, Minnesota). Site preparation and management were as described in Chapter 1.

Data collection and sampling

In 2010 and 2011, censuses were conducted for all individuals belonging to deliberately-sown species. Early snowfall precluded censusing 27 plots at St. Paul. In 2012, full censuses were

conducted at Morris, St. Paul, and Waseca. The Staples plots were not censused due to snow cover. Aboveground biomass was then harvested from 3 randomly-chosen plots per switchgrass strain at St. Paul, Waseca, and Staples. Plots at Morris were not harvested because very few switchgrass plants were present. Material was clipped at 4 cm above the soil surface, sorted to species, dried at 60 °C until no further loss of weight was observed. Samples weighing < 0.1 g were assigned a value of 0.05 g.

Community performance and composition metrics

For analysis, plant species were grouped in three ways: all species undifferentiated as to origin; as species deliberately sown into the plots versus those not sown; and as native versus exotic species, where “exotic” was defined as originating outside the Midwestern U.S. (USDA NRCS, 2015). Within these groups, community performance was measured as abundance (individuals m⁻²) and aboveground biomass (g m⁻²). Community diversity was characterized as species richness (m⁻²), species diversity, and species evenness. Diversity and evenness were estimated using Brillouin’s indices, which are appropriate for fully-censused communities (Magurran, 2004). Brillouin’s diversity index (HB) = $\{ \ln(N!) - \sum_i \ln(n_i!) \} / N$, where N is total number of individuals in the plot and n is the number of individuals for the i th species. Brillouin’s diversity values range from 0 for monospecific plots to approximately 4.5 in highly diverse systems (Magurran, 2004). Brillouin’s evenness index (HBE) is the ratio of HB:HB_{max}, with HB_{max} = $(1/n) * \ln \{ N! / [(X!)^{S-r} * ((Y!)^r] \}$, where S is species richness, X is the integer portion of N/S , r is the remainder of N/S , and $Y = X + 1$ (Magurran, 2004). Brillouin’s evenness indices can take any positive value equal to or less than 1; if fewer than 2 species are present, HBE values are not calculable. A value of 1 indicates that all species present have exactly equal abundances. Performance and composition values for each plot were calculated both including and excluding switchgrass. When switchgrass stand density or biomass were used as explanatory variables, the responses excluded switchgrass.

Switchgrass performance metrics

Switchgrass performance was measured as establishment, persistence, final (third-year) stand density, and biomass. Establishment was measured as the number of new recruits at the ends of the first and second growing seasons. Second-year recruits were distinguished from previously-established individuals by the development of the crowns and the absence of stubble from senesced culms. Persistence was estimated as interannual differences in stand density

(switchgrass individuals m^{-2}). Switchgrass biomass was measured as aboveground, current-year material and was analyzed both in absolute terms and as a proportion of community biomass.

Analysis

Community composition, performance, and diversity

Principal components analyses (PCA) were performed on the 2012 census and biomass data to descriptively compare the plant communities across sites, and to assess whether plots sown with cultivars versus ecotypes or with single- versus multi-foundation strains clustered in species-space. To reduce the influence of species with large numbers of individuals, abundance data were log-transformed (Waite, 2000); PCAs were then performed on variance-covariance matrices using the *vegan* package (Oksanen *et al.*, 2013) in R (v. 3.1.0, R Core Team 2013). In the resulting ordination diagrams, data points were coded by field site and by switchgrass population characteristics (breeding-history, foundation-number, strain). Apparent patterns in the scores distributions of these PCAs were examined using MANOVA with Pillai's Trace on both PCs jointly, ANOVA on PC1 and PC2 individually, and Student-Newman-Keuls *a posteriori* tests (Zar, 1999). Additional MANOVAs were performed on the joint responses with switchgrass third-year stand density and biomass each used as a single predictor.

Univariate (UV) linear models were used to analyze the effects of switchgrass characteristics (breeding history, foundation-number, strain) and performance (stand density, biomass) on the above-listed measures of community performance and diversity. Univariate models were also used to analyze the effects of switchgrass characteristics on additional measures of switchgrass performance (establishment, persistence, and biomass). These UV models included main effects and all two-way interactions; higher order interactions were excluded because of associated difficulties in interpretation. Sites were analyzed collectively and individually; in the former case, "site" was a fixed effect. Correlated explanatory variables ($r > 0.7$, Neter *et al.*, 1990) were segregated into separate analyses. All residuals were visually assessed for compliance with model assumptions. In marginal cases, non-normality was tested with Shapiro-Wilk's W and heteroscedasticity with Bartlett's, Levene's, or Fligner's tests, as appropriate. The residuals from parametric models of transformed data generally approximated normality and homoscedasticity. Fixed effect ANOVAs are quite robust to violation of these assumptions, especially with equal or approximately equal sample sizes (Glass *et al.*, 1972). Due to this robustness, and because candidate generalized linear models (GLMs) were generally either over- or underdispersed, methods that assume normally distributed residuals were utilized.

After characterizing species as deliberately sown/unsown, and as native/exotic, multivariate (MV) analyses were used to model the joint abundance, biomass, richness, HB, and HBE values of these differentiated communities. Individual responses were visually assessed for UV normality; residuals were tested for heteroscedasticity as described above and for non-normality using the MV Shapiro test (*mvnormtest*) from the *RV AideMemoire* package in R (Hervé, 2015). For all analyses, count and biomass responses were log- and square-root transformed, respectively; HB and HBE values were not transformed.

Switchgrass performance

To evaluate the extent to which switchgrass population characteristics affected performance, establishment, final stand density, persistence, and biomass were modeled as functions of breeding history and foundation-number or switchgrass strain, both within sites and jointly across them. Third-year census data and biomass samples were not collected at Staples and Morris, respectively; those sites were excluded from some analyses. Persistence, defined as the change in switchgrass stand density between specified time points, was modeled using profile analyses (Tabachnik & Fidell, 2013). Differences in stand density between two growing seasons were assessed using Mann-Whitney-Wilcoxon rank-sums tests, because transformed data violated parametric assumptions. The effects of switchgrass characteristics on persistence and on multiple persistence values (i.e., parallelism) were tested with UV ANOVA and MANOVA, respectively. Prior to these analyses, pairwise Pearson correlations were calculated for the three persistence measures ($\text{density}_{2011-2010}$, $\text{density}_{2012-2011}$, $\text{density}_{2012-2010}$). At the three sites for which census data were available for all three years, $\text{density}_{2011-2010}$ and $\text{density}_{2012-2010}$ were strongly correlated ($r > 0.88$); accordingly, the former measure was excluded from the MV response. For all models of switchgrass performance, candidate models were compared and *a posteriori* tests were conducted as previously described. Transformations for establishment and final stand density values, absolute biomass, and proportional biomass were log (+1), square-root, and arcsine-square root, respectively. Persistence values were not transformed.

Results

Community impacts of switchgrass

Ordinations of the 2012 census and biomass data performed jointly across sites indicated that the sites segregated strongly along the first two principal components (PC) (Fig. 2-1A-B). When sites were analyzed individually, no patterns in community composition were observed

relative to switchgrass characteristics for either census or biomass ordinations (Fig. 2-2A-F, Fig. 2-3A-F). Univariate and MV ANOVAs confirmed that switchgrass characteristics and performance generally exerted weak and inconsistent effects on ordination scores (Table 2-2). However, two noteworthy results from the biomass ordinations were observed: cultivars differentiated from ecotypes at Staples (Table 2-2, Fig. 2-4A) and multi-foundation ecotypes differentiated from the other groups at St. Paul (Table 2-2, Fig. 2-4B).

The effects of switchgrass characteristics and performance on community performance and diversity were analyzed separately for the undifferentiated, the sown/unsown, and the native/exotic communities at each site. Little evidence was found that the abundance values, biomass, or diversity of undifferentiated communities were affected by switchgrass population characteristics or by switchgrass abundance or biomass. However, ecotypes were associated with modestly higher community abundances than cultivars at St. Paul (Table 2-3, Fig 2-5).

Performance measures for sown/unsown and native/exotic communities were affected by switchgrass characteristics or performance (Tables 2-4, 2-5); effects were inconsistent among sites and generally small. Several exceptions were observed, however. Abundances of sown species were 30% higher for multi-foundation cultivars than other switchgrass groups at Waseca (Table 2-4, Fig. 2-6A). Abundances of unsown species were approximately 30% lower for cultivars than ecotypes at St. Paul (Fig. 2-6B); a similar pattern occurred with exotic-species abundances at that site (Tables 2-4, 2-5). Mean values for sown- and native-species biomass were 40% higher for multi- than single-foundation ecotypes at Waseca (Tables 2-4, 2-5, Fig. 2-7A) although the pertinent interactions between breeding history and foundation-number were not significant at $\alpha = 0.05$. Multi-foundation ecotypes were associated with significantly and substantially greater exotic-species biomass than were other switchgrass groups at St. Paul (Table 2-5, Fig. 2-7B). In contrast, multi-foundation switchgrass was associated with unsown- and exotic-species biomass values that were significantly lower than those associated with single-foundation strains at Staples (Tables 2-4, 2-5, Fig. 2-7C). Exotic biomass differed among switchgrass strains at two sites (Table 2-5, Fig. 2-8) but no patterns were observed.

Diversity metrics for sown/unsown and native/exotic communities were affected by switchgrass characteristics or performance in a few cases (Tables 2-4, 2-5); effects were inconsistent and either non-significant or small. Unsown and exotic species richness values ranged two- to three-fold across the 12 switchgrass strains at Waseca (Tables 2-4, 2-5, Fig. 2-9) but no pattern was evident. Sown-species HB was significantly higher for multi- than for single-foundation strains at Waseca (Table 2-4) but the effect size was modest. No other effects of

switchgrass attributes on HB or HBE were observed, possibly because of low diversity at all sites. No evidence was found for any effect of switchgrass on HBE values.

For sites analyzed jointly, the effects of switchgrass characteristics on community performance and diversity were generally weak, whether the community was undifferentiated or grouped into sown/unsown or native/exotic species (Tables 2-3, 2-4, 2-5). Although ecotypes were associated with greater exotic-species richness than were cultivars, the effect was very small (Table 2-5, Fig. 2-10).

Switchgrass performance

Switchgrass performance was characterized as establishment, third-year stand density, persistence, and biomass. Most effects of switchgrass characteristics on these performance measures were modest and inconsistent among sites; however, cultivars significantly and substantially exceeded ecotypes in first-year establishment and in third-year stand density (Table 2-6, Figs. 2-11, 2-12). First-year establishment and third-year stand density also varied considerably among switchgrass strains within each site (Table 2-6, Figs. 2-13, 2-14). Throughout the study, the numbers of switchgrass individuals at both Morris and Waseca were very small. The large proportion of zeroes resulted in models for the third-year responses that deviated strongly from parametric assumptions, and p -values should be interpreted cautiously.

Switchgrass persistence values were generally negative, indicating declines in stand density over time. The declines were substantial between the first and second years but minor between the second and third (Table 2-7, Fig. 2-15). There was little evidence that persistence was affected by switchgrass breeding history or foundation number (Table 2-8). However, ecotypes had significantly greater persistence than cultivars between the first and third years at St. Paul (Table 2-8, Fig. 2-16). This was partially caused by delayed germination for some ecotypes. Persistence from the first to the third year varied considerably among switchgrass strains and inconsistently among sites (Table 2-8, Fig. 2-17).

The effects on switchgrass biomass of breeding history, foundation number and strain were generally weak and varied across sites (Table 2-6). However, both absolute and proportional biomass of cultivars exceeded that of ecotypes at two sites (Fig. 2-18). Mean values of both absolute and proportional biomass were approximately 50% higher for single- than for multi-foundation strains at St. Paul; the differences, although suggestive, were not statistically significant (Table 2-6). Strains significantly differed in biomass within and across sites (Table 2-6) but no patterns emerged.

Discussion

Large (re)constructed bioenergy grasslands and ecological restorations are likely to increase in number during the coming years (Hobbs *et al.*, 2011, Blank *et al.*, 2014). To date, few studies have examined the risks associated with translocating native species on the scales that such efforts will require (Kwit & Stewart, 2012). These risks include: failure of the translocated population due to non-establishment or low adaptive potential; biodiversity loss resulting from over-dominance by strongly competitive translocated populations; and gene flow from translocated populations that negatively affects local remnant populations (Zavaleta & Hulvey, 2004; Baer *et al.*, 2005; McKay *et al.*, 2005). In this study, three aspects of these risks were examined: performance of translocated switchgrass populations, switchgrass impacts on plant-community diversity, and indirect evidence for adaptive potential. Switchgrass cultivars perform more strongly than ecotypes but there was no evidence that this superior performance translates into adverse effects on plant diversity.

The results of this experiment suggest that the use of adequately locally-adapted switchgrass cultivars in multifunctional grasslands could mitigate several associated risks. Such grasslands can produce both bioenergy and other ecosystem services (Fletcher *et al.*, 2011; Blank *et al.*, 2014); accordingly, high native plant diversity is desired because it supports both objectives (Tilman *et al.*, 2006; Cardinale *et al.*, 2007; Cook-Patton *et al.*, 2011). Switchgrass cultivars, which were found to exceed ecotypes in establishment, stand density, and yield, could reduce the risk of population non-establishment while producing greater biomass and posing no greater of a threat to plant-community diversity.

In ecological restorations, where high yields are generally not a priority, the primary benefit of using cultivars may arise from their higher early-stage establishment. Slow or weak establishment of restored populations may increase vulnerability to colonization by invasive species and subsequent biodiversity loss (Zavaleta & Hulvey, 2004). Consistent with other studies (Gustafson *et al.*, 2004a; Klopff *et al.*, 2014), the current work indicates that cultivars may reduce that risk relative to ecotypes. When exotic C₃ grasses were strongly dominant, some ecotypes failed to establish or persist; however, under such intense competition, some cultivars also failed. When competition is moderate, ecotypes can perform similarly to cultivars and are associated with similar plant communities. With adequate site preparation and weed control, ecotypes may produce equivalent restoration results to cultivars.

Accordingly, decisions about restoration plant-material sources can prioritize other important considerations related to genetic variation and gene flow. Despite the anticipated

benefits of multifunctional grasslands, a substantial amount of bioenergy production is expected to be monocultural (McLaughlin & Kszos, 2005). This may result in landscape-scale homogeneity of biofuel crops (Robertson *et al.*, 2008) and accompanying risks that include pest and pathogen infestations (Hartman *et al.*, 2011). The judicious use of local ecotypes could buffer cultivated, restored, and remnant populations from these adversities as well as reducing serious risks associated with gene flow between translocated and remnant populations.

In this experiment, switchgrass cultivars had higher establishment, third-year stand density, and biomass than ecotypes, although substantial variation occurred in both groups and across sites. Other published studies have observed similar patterns in switchgrass performance (Casler, 2005; Wilsey, 2010). Given the higher establishment rates observed in cultivars, lower persistence is not surprising; delayed germination for some ecotypes resulted in positive persistence values. However, this effect was not enough for ecotypes to match cultivars in third-year density.

Despite cultivars' stronger performance, they were not found to adversely affect sown or native biodiversity relative to ecotypes. This is consistent with several other studies. For example, Gibson *et al.* (2013) sowed cultivar and ecotypic sources of *A. gerardii*, *S. nutans*, and *S. scoparium* into common gardens that were simultaneously sown with varied assemblages of C3 and C4 grasses, legumes, and non-leguminous forbs. Measures of abundance and composition differed among species pools but not between cultivars and ecotypes (Gibson *et al.*, 2013). In paired experiments in Illinois and Kansas, species density and diversity in cultivar treatments were at least equal to those in plots containing ecotypes (Klopf *et al.*, 2014). Aboveground net primary productivity did not significantly differ between experimental prairie plots containing a regional *S. nutans* cultivar and those with local Kansas ecotypes (Baer *et al.*, 2014). In contrast, an experiment that used 'Blackwell' switchgrass near its site of origin found that plant-community diversity decreased as switchgrass percent-cover increased; however, this was attributed to experimental nitrogen additions (Baer *et al.*, 2005).

In addition to comparing cultivars and ecotypes, the current work examined the effect of switchgrass strain on performance and community impact. Other studies have reported that strains perform variably across sites; for example, population x location interactions have been found to account for 5-40% of the variance in mean values of survival, height, and aboveground biomass (Casler *et al.*, 2004; Casler, 2005). Consistent with these studies, the current work indicates that some strains performed poorly at most sites. It is possible that no sites contained conditions to which the strains were well-adapted or that site-specific conditions affected the

maternal performance and seed provisioning. Results from this experiment strongly indicate that prior knowledge of a strain's likely performance for a given region is critical to successful population establishment.

No evidence was found for stronger interannual or cross-site performance in multi-foundation strains, which are assumed to have greater genetic variation than their single-foundation counterparts. There are several non-exclusive explanations for this absence of evidence. The sites may have been insufficiently different for the presumptively adaptive and greater genetic variation of the multi-foundation strains to contribute to stand performance. Interannual variability may have been insufficiently severe to reduce the relative performance of single-foundation strains. The study may have been too short for multi-foundation strains to realize their greater adaptive potential, if present. Finally, the multi-foundation strains may not have contained substantially greater genetic variation or may have been maladapted.

Some study limitations may also have contributed to the lack of foundation-number effect. Although overall sample sizes were large, the foundation-number groups contained only five or seven strains. More importantly, assignment of strains to the single- or multi-foundation group was based on uncertain and sometimes conflicting information. Variability in switchgrass performance across sites and years may have obscured any patterns that were present. In addition, third-year stand density and biomass data were only available for three sites; at two of these, switchgrass presence was low. These factors limit the extent of inference that can be drawn.

In order to be most relevant to prairie restoration practice in Minnesota, low switchgrass seeding densities were used in this experiment. With respect to reconstructions using substantially higher switchgrass seeding rates, these findings should be interpreted cautiously. Higher densities might have resulted in lower community abundances or diversity through the competitive exclusion of other plants or species, especially in light of cultivars' superior first-year establishment rates. The same dynamic, however, could also increase intraspecific competition and juvenile mortality within cultivars; ecotypes might then have comparatively denser stands and higher persistence. In addition to altering the relative performance of switchgrass populations, this dynamic could alter impacts on community composition and performance.

Two limitations of this work relate to duration and statistical power. Prairie communities can take 6-10 years to fully establish, depending on species composition and management (Schramm, 1990); the current experiment focused only on initial community establishment. A longer-term study would be required to assess, for example, whether delayed ecotypic establishment translates into permanently lower ecotypic productivity. Additional data could also

increase statistical power; despite substantial replication, inherent variability hindered detection of differences.

Site conditions merit a final comment. Other studies have concluded that propagule pressure from unsown species strongly affects community trajectory (Yurkonis, 2013); results presented here are consistent with these studies and may indicate that the unsown-species seedbank was strongly influenced by land-use history. Previous usage of the experimental sites ranged from row-crop cultivation to pasturage. At the latter site, which was dominated by exotic C3 grasses, perennial forbs and legumes, all switchgrass strains performed poorly regardless of source-population characteristics. This study underscores the need for adequate and possibly repeated site preparation. Absent such preparation, at least some desired species will fail to establish, jeopardizing the fulfillment of project biodiversity goals.

Conclusions

The performance of switchgrass cultivars is superior to that of ecotypes during the early stages of development in experimental prairie communities. Superior cultivar performance did not translate to decreased diversity of sown or native species; additionally, cultivars were associated with lower presence of unsown and exotic species than ecotypes. If adequately adapted to local conditions, switchgrass cultivars may offer an acceptable balance between reduced likelihood of stand failure and over-dominance that impairs community biodiversity. However, observed differences between ecotype and cultivar performance were modest. With respect to the full constellation of risks associated with cultivating switchgrass for biofuels, ecotypes may offer a superior compromise without strongly decreasing yield.

Where biomass yield is not a project goal, cultivars and ecotypes deliver similar restoration outcomes, under conditions of moderate competition from unsown species. However, some ecotypes may fail to establish or persist at the low seeding densities used in this study. Active management may be required during the early stages of restoration, especially if competition is severe. In the absence of a clear rationale for cultivar use, germplasm sourcing decisions should prioritize the enhancement of landscape-scale switchgrass variation and management of risks associated with gene flow between translocated and remnant populations.

Multi-foundation strains, which presumably contain greater genetic variation, were not found to have stronger interannual or cross-site performance than single-foundation strains. Insufficient variation in conditions, low statistical power, a lack of or maladaptive genetic variation, or mistaken assignment of foundation-number may explain the lack of difference.

There is considerable interest in enhancing site- and landscape-scale genetic variation as a way to increase resilience under conditions of rapid environmental change and reduce risks associated with population homogeneity. One strategy is to generate strains by combining foundation populations. Additional research is needed on the extent to which this technique can contribute to quantitative-genetic variation in switchgrass strains.

These findings should not be interpreted as supporting the widespread use of cultivars in areas where small, isolated, switchgrass remnants exist. The population-level fitness of those remnants and their contribution to landscape-scale genetic heterogeneity should be assessed prior to large-scale switchgrass cultivation. The value of wild switchgrass populations as genetic resources may outweigh potential efficiencies conferred by cultivar use. Ecological restorations and bioenergy grasslands will become increasingly common and with them, the risks associated with translocating native species. Assessment and management of these risks is necessary for full realization of the benefits of these environmental interventions.

Tables

Table 2-1: Community seed mix; all species produced by Prairie Restorations, Inc. (Princeton, MN). Percent germination includes dormant seed.

Species	Common Name	% pure seed (by weight)	% germination	% dormant	Source location
<i>Andropogon gerardii</i>	Big bluestem	35.13	86	81	MN
<i>Sorghastrum nutans</i>	Indiangrass	25.75	88	80	MN
<i>Schizachyrium scoparium</i>	Little bluestem	13.49	84	54	MN
<i>Bouteloua curtipendula</i>	Sideoats grama	8.99	63	27	MN
<i>Elymus canadensis</i>	Canada wildrye	5.96	95	0	MN
<i>Rudbeckia hirta</i>	Black-eyed Susan	15.97	96	19	IA
<i>Verbena stricta</i>	Hoary vervain	14.03	83	83	MN
<i>Dalea purpurea</i>	Purple prairie clover	13.99	92	14	MN
<i>Heliopsis helianthoides</i>	Ox-eye	5.97	92	46	MN
<i>Amorpha canescens</i>	Leadplant	5.78	50	42	MN
<i>Monarda fistulosa</i> var <i>fistulosa</i>	Wild bergamot	3.80	59	3	MN
<i>Solidago rigida</i> ssp. <i>humilis</i>	Stiff goldenrod	3.78	69	2	MN
<i>Dalea candida</i>	White prairie clover	3.54	91	83	MN
<i>Zizia aurea</i>	Golden alexanders	2.86	68	66	MN
<i>Liatris pycnostachya</i>	Prairie blazing star	2.83	79	65	MN
<i>Agastache foeniculum</i>	Blue giant hyssop	2.73	76	0	MN
<i>Symphyotrichum laeve</i>	Smooth blue aster	2.40	58	22	MN
<i>Symphyotrichum oolentangiense</i>	Sky-blue aster	2.00	90	90	WI
<i>Solidago ptarmicoides</i>	Prairie goldenrod	1.92	60	22	MN
<i>Lespedeza capitata</i>	Hairy lespedeza	1.91	38	0	MN
<i>Solidago speciosa</i>	Showy goldenrod	1.78	46	1	MN
<i>Symphyotrichum ericoides</i>	White heath aster	0.97	96	96	IA
<i>Achillea millefolium</i>	Yarrow	0.95	85	85	MN
<i>Desmodium canadense</i>	Showy tick-trefoil	0.94	45	2	MN
<i>Solidago nemoralis</i>	Gray goldenrod	0.82	55	55	MN
<i>Potentilla arguta</i>	Tall cinquefoil	0.81	88	53	MN
<i>Coreopsis palmata</i>	Stiff tickseed	0.69	61	58	MN
<i>Asclepias syriaca</i>	Common milkweed	0.48	76	76	MN
<i>Helianthus pauciflorus</i>	Stiff sunflower	0.45	76	76	MN

Table 2-2: ANOVA and MANOVA results for the effects of switchgrass population characteristics on PCA scores. Biomass data for Morris and census data for Staples are not available. V: Pillai's Trace. Bold italicized text: $p < 0.1$. Bold text: $p < 0.05$.

	V	MV models F(df)	p	PC1 F(df)	p	PC 2 F(df)	p
CENSUS							
Morris							
Breeding history	0.0262	0.902 (2, 67)	0.41	0.467 (1, 68)	0.50	1.32 (1, 68)	0.25
Foundation-number	0.0255	0.877 (2, 67)	0.42	1.71 (1, 68)	0.20	0.657 (1, 68)	0.42
Breed. x found.	0.000852	0.029 (2, 67)	0.97	0.00300 (1, 68)	0.96	0.0557 (1, 68)	0.81
Strain	0.239	0.74 (22, 120)	0.79	0.827 (11, 60)	0.61	0.654 (11, 60)	0.78
St. Paul							
Breeding history	0.0165	0.560 (2, 67)	0.57	0.663 (1, 68)	0.42	0.442 (1, 68)	0.51
Foundation-number	0.0657	2.36 (2, 67)	0.10	3.99 (1, 68)	0.05	0.179 (1, 68)	0.67
Breed. x found.	0.0314	1.08 (2, 67)	0.34	1.99 (1, 68)	0.16	0.174 (1, 68)	0.68
Strain	0.333	1.09 (22, 120)	0.37	1.28 (11, 60)	0.26	0.913 (11, 60)	0.53
Waseca							
Breeding history	0.0405	1.41 (2, 67)	0.25	2.86 (1, 68)	0.095	0.00830 (1, 68)	0.93
Foundation-number	0.0423	1.48 (2, 67)	0.24	0.0927 (1, 68)	0.76	2.67 (1, 68)	0.11
Breed. x found.	0.00409	0.138 (2, 67)	0.87	0.262 (1, 68)	0.61	0.0180 (1, 68)	0.89
Strain	0.514	1.88 (22, 120)	0.016	1.72 (11, 60)	0.09	2.05 (11, 60)	0.04
BIOMASS							
Staples							
Breeding history	0.328	7.55 (2, 31)	0.0021	0.807 (1, 32)	0.36	14.7 (1, 32)	0.00056
Foundation-number	0.972	1.67 (2, 31)	0.20	0.978 (1, 32)	0.33	4.69 (1, 32)	0.038
Breed. x found.	0.105	1.82 (2, 31)	0.18	3.51 (1, 32)	0.07	0.273 (1, 32)	0.60
Strain	0.971	2.06 (22, 48)	0.019	2.00 (11, 24)	0.08	2.11 (11, 24)	0.06
St. Paul							
Breeding history	0.0318	0.509 (2, 31)	0.61	0.0889 (1, 32)	0.77	1.00 (1, 32)	0.32
Foundation-number	0.0893	1.52 (2, 31)	0.23	2.74 (1, 32)	0.11	0.235 (1, 32)	0.63
Breed. x found.	0.174	3.27 (2, 31)	0.051	5.05 (1, 32)	0.032	1.23 (1, 32)	0.28
Strain	0.715	1.21 (22, 48)	0.28	1.13 (11, 24)	0.39	1.31 (11, 24)	0.28
Waseca							
Breeding history	0.159	2.94 (2, 31)	0.068	2.79 (1, 32)	0.10	2.72 (1, 32)	0.11
Foundation-number	0.00732	0.114 (2, 31)	0.89	0.0179 (1, 32)	0.89	0.00420 (1, 32)	0.95
Breed. x found.	0.0421	0.681 (2, 31)	0.51	1.343 (1, 32)	0.25	0.0217 (1, 32)	0.88
Strain	0.736	1.27 (22, 48)	0.24	1.9927 (11, 24)	0.077	0.762 (11, 24)	0.67

Table 2-3: ANOVA results on the effects of switchgrass population characteristics and performance on measures of undifferentiated community performance and diversity. Joint-site biomass analyses used data from Staples, St. Paul, and Waseca; all other joint analyses used data from Morris, St. Paul, and Waseca. Bold italicized text: $p < 0.1$. Bold text: $p < 0.05$. Adjusted R^2 values given if $p < 0.05$. HB: Brillouin diversity index. HBE: Brillouin evenness index.

	Community abundance		Community biomass		Species richness		HB		HBE	
	F (df)	<i>p</i>	F (df)	<i>p</i>	F (df)	<i>p</i>	F (df)	<i>p</i>	F (df)	<i>p</i>
JOINT										
site	106 (2, 204)	< 0.0001	129 (2, 98)	<0.0001	19.0 (2, 206)	< 0.0001	226 (2, 204)	< 0.0001	204 (2, 202)	< 0.0001
breeding history	0.299 (1, 204)	0.59	0.0817 (1, 98)	0.78	0.833 (1, 206)	0.36	0.399 (1, 204)	0.53	0.0789 (1, 202)	0.78
foundation-number	0.00140 (1, 204)	0.97	0.081 (1, 98)	0.78	0.771 (1, 206)	0.38	0.166 (1, 204)	0.68	0.0783 (1, 208)	0.78
site x breed.	1.831 (2, 204)	0.16	1.26 (2, 98)	0.29	0.102 (2, 206)	0.90	1.07 (2, 204)	0.35	2.000 (2, 202)	0.14
site x found.	0.908 (2, 204)	0.40	0.136 (2, 98)	0.87	3.21 (2, 206)	0.042	1.59 (2, 204)	0.21	0.118 (2, 202)	0.89
breed. x found.	0.69 (1, 204)	0.41	1.60 (1, 98)	0.21	0.685 (1, 206)	0.41	0.000 (1, 204)	0.99	0.126 (1, 202)	0.72
site	105 (2, 210)	< 0.0001	124 (2, 72)	< 0.0001	32.3 (2, 180)	< 0.0001	228 (2, 180)	< 0.0001	206 (2, 178)	< 0.0001
strain	0.0099 (1, 210)	0.92	0.873 (11, 72)	0.57	0.995 (11, 180)	0.45	1.42 (11, 180)	0.17	1.270 (11, 178)	0.25
site x strain	0.904 (2, 210)	0.41	0.755 (22, 72)	0.77	1.20 (22, 180)	0.25	0.871 (22, 180)	0.63	0.936 (22, 128)	0.55
site	108 (2, 210)	< 0.0001	0.0490 (1, 68)	0.83	10.09 (2, 210)	< 0.0001	130 (2, 210)	< 0.0001	141 (2, 208)	< 0.0001
stand density	1.63 (1, 210)	0.20	2.084 (1, 68)	0.15	0.230 (1, 210)	0.63	0.0921 (1, 210)	0.76	0.0578 (1, 208)	0.81
site x stand density	2.91 (2, 210)	0.056	0.516 (1, 68)	0.48	1.14 (2, 210)	0.32	1.083 (2, 210)	0.34	1.43 (2, 208)	0.25
site	2.56 (1, 68)	0.11	119 (2, 102)	<0.0001	0.363 (1, 68)	0.55	7.86 (1, 68)	0.0066	2.84 (1, 68)	0.097
biomass	0.0862 (1, 68)	0.77	1.455 (1, 102)	0.23	0.869 (1, 68)	0.35	0.0005 (1, 68)	0.98	0.106 (1, 68)	0.75

site x biomass	0.250 (1, 68)	0.62	0.647 (2, 102)	0.53	0.324 (1, 68)	0.57	0.041 (1, 68)	0.84	0.168 (1, 68)	0.68
MORRIS										
breeding history	0.858 (1, 68)	0.36			0.0607 (1, 68)	0.81	0.381 (1, 68)	0.54	1.69 (1, 66)	0.20
foundation-number	0.670 (1, 68)	0.41			1.49 (1, 68)	0.23	0.0266 (1, 68)	0.87	0.100 (1, 66)	0.75
breed. x found.	0.885 (1, 68)	0.35	Data not available		0.0867 (1, 68)	0.77	1.37 (1, 68)	0.25	2.01 (1, 66)	0.16
strain	1.31 (11, 60)	0.24			0.375 (11, 60)	0.96	0.913 (11, 60)	0.53	1.117 (11, 58)	0.33
stand density adj R ²	0.0132 (1,70) - 0.014	0.91			0.639 (1, 70)	0.43	1.35 (1, 70)	0.25	1.79 (1, 68)	0.19
biomass	Data not available				Data not available		Data not available		Data not available	
STAPLES										
breeding history			0.379 (1, 32)	0.54						
foundation-number			0.177 (1, 32)	0.68						
breed. x found.	Data not available				Data not available		Data not available		Data not available	
strain			1.39 (11, 24)	0.24						
stand density			Data not available							
biomass			0.563 (1, 34)	0.46						
ST. PAUL										
breeding history	7.64 (1, 68)	0.0074	1.47 (1, 32)	0.23	0.103 (1, 68)	0.75	0.635 (1, 68)	0.43	1.400 (1, 68)	00.24
foundation-number	0.0257 (1, 68)	0.87	0.448 (1, 32)	0.51	2.72 (1, 68)	0.10	0.0413 (1, 68)	0.39	0.0848 (1, 68)	0.77
breed. x found.	0.0814 (1, 68)	0.78	0.421 (1, 32)	0.52	0.304 (1, 68)	0.58	0.193 (1, 68)	0.66	1.98 (1, 68)	0.66
strain	0.93 (11, 60)	0.52	0.190 (11, 24)	0.99	1.93 (11, 60)	0.053	0.899 (11, 60)	0.55	0.354 (11, 60)	0.99
stand density	0.827 (1, 70)	0.37	1.02 (1, 34)	0.32	0.0054 (1, 70)	0.94	0.136 (1, 70)	0.71	0.577 (1, 70)	0.45

biomass	0.0945 (1, 34)	0.76	1.66 (1, 34)	0.21	0.917 (1, 34)	0.35	0.0036 (1, 34)	0.95	0.206 (1, 34)	0.65
WASECA										
breeding history	0.0679 (1, 68)	0.80	0.907 (1, 32)	0.35	0.168 (1, 68)	0.68	1.99 (1, 68)	0.16	0.892 (1, 68)	0.35
foundation- number	0.900 (1, 68)	0.34	0.253 (1, 32)	0.62	4.05 (1, 68)	0.05	3.76 (1, 68)	0.06	0.119 (1, 68)	0.73
breed. x found.	0.454 (1, 68)	0.50	2.14 (1, 32)	0.15	1.07 (1, 68)	0.31	1.60 (1, 68)	0.21	0.405 (1, 68)	0.53
strain	1.69 (11, 60)	0.098	1.84 (11, 24)	0.10	1.39 (11, 60)	0.20	1.52 (11, 60)	0.15	1.36 (11, 60)	0.22
stand density	2.88 (1, 70) R ² = 0.03	0.094	2.00 (1, 34)	0.166	3.12 (1, 70) R ² = 0.03	0.082	0.205 (1, 70)	0.65	0.176 (1, 70)	0.68
biomass	0.2402 (1, 34)	0.62	1.38 (1, 34)	0.25	0.209 (1, 34)	0.65	0.0423 (1, 34)	0.84	0.0929 (1, 34)	0.76

Table 2- 4: Results of UV and MV ANOVAs testing the effects of switchgrass population characteristics and performance on deliberately-sown and unsown community metrics. Joint-site biomass analyses include data from Staples, St. Paul, Waseca; all other joint analyses include data from Morris, St. Paul, Waseca. Bold text: $p < 0.05$. Bold italicized text: $p < 0.1$.

	Sown Abundance		Unsown Abundance			MV Abundance	
	F(df)	<i>p</i>	F(df)	<i>p</i>	V	F(df)	<i>p</i>
JOINT							
site	213 (2, 206)	< 0.001	48.6 (2, 206)	< 0.0001	0.889	82.4 (4, 412)	< 0.001
breeding history	0.0247 (1, 206)	0.87	0.485 (1, 206)	0.49	0.00539	0.556 (2, 205)	0.57
foundation number	0.0476 (1, 206)	0.83	2.44 (1, 206)	0.12	0.0122	1.267 (2, 205)	0.28
site x breed.	0.182 (2, 206)	0.83	1.24 (2, 206)	0.29	0.0112	0.581 (4, 412)	0.68
site x found.	2.35 (2, 206)	0.098	0.459 (2, 206)	0.63	0.0226	1.178 (4, 412)	0.32
found. x breed.	0.241 (1, 206)	0.62	0.353 (1, 206)	0.55	0.00218	0.224 (2, 205)	0.80
site	69.2 (2, 180)	< 0.0001	152 (2, 180)	< 0.0001	0.783	57.8 (4, 360)	< 0.0001
strain	0.817 (11, 180)	0.62	1.55 (11, 180)	0.12	0.135	1.19 (22, 360)	0.26
site x strain	0.704 (22, 180)	0.83	1.79 (22, 180)	0.021	0.260	1.22 (44, 360)	0.17
site	72.9 (2, 210)	<0.0001	142 (2, 210)	<0.0001	0.663	52.0 (4, 420)	<0.0001
stand density	3.15 (1, 210)	0.077	1.37 (1, 210)	0.24	0.0221	2.36 (2, 209)	0.097
site x stand	1.11 (2, 210)	0.33	1.65 (2, 210)	0.20	0.0245	1.30 (4, 420)	0.27
site	0.247 (1, 68)	0.62	7.36 (1, 68)	0.0084	0.0893	3.28 (2, 67)	0.044
biomass	0.0057 (1, 68)	0.94	0.0209 (1, 68)	0.89	0.000471	0.0158 (2, 67)	0.98
site x biomass	1.20 (1, 68)	0.28	0.049 (1, 68)	0.83	0.0173	0.59 (2, 67)	0.56
MORRIS							
Breeding history	0.763 (1, 68)	0.39	0.638 (1, 68)	0.43	0.0230	0.789 (2, 67)	0.46
Foundation-number	1.27 (1, 68)	0.26	1.29 (1, 68)	0.26	0.0323	1.12 (2, 67)	0.33
Breed. x found.	0.790 (1, 68)	0.38	0.657 (1, 68)	0.42	0.0238	0.815 (2, 67)	0.45
Strain	0.507 (11, 60)	0.89	1.52 (11, 60)	0.15	0.263	0.825 (22, 120)	0.69
Stand density	0.362 (1, 70)	0.55	0.0009	0.99	0.00554	0.192 (2, 69)	0.83
ST. PAUL							
Breeding history	0.621 (1, 68)	0.43	7.42 (1, 68)	0.0082	0.100	3.73 (2, 67)	0.029
Foundation-number	0.172 (1, 68)	0.68	0.708 (1, 68)	0.40	0.00729	0.246 (2, 67)	0.78
Breed. x found.	0.383 (1, 68)	0.54	0.193 (1, 68)	0.66	0.00978	0.331 (2, 67)	0.72
Strain	0.723 (11, 60)	0.71	1.51 (11, 60)	0.15	0.346	1.10 (2, 120)	0.31
Stand density	1.237 (1, 70)	0.27	4.95 (1, 70)	0.029	0.0966	3.690 (2, 69)	0.030
	adj R ² = 0.003		adj R ² = 0.0526				
Biomass	0.0756 (1, 34)	0.79	0.0164 (1, 34)	0.90	0.00336	0.0600 (2,33)	0.95

WASECA								
Breeding history	0.924 (1, 68)	0.34	0.205 (1, 68)	0.65	0.0145	0.493 (2, 67)	0.61	
Foundation-number	5.67 (1, 68)	0.02	0.133 (1, 68)	0.72	0.0847	3.10 (2, 67)	0.052	
Breed. x found.	4.94 (1, 68)	0.030	0.0001 (1, 68)	0.99	0.0700	2.52 (2, 67)	0.088	
Strain	1.42 (11, 60)	0.18	1.91 (11, 60)	0.056	0.472	1.69 (22, 120)	0.039	
Stand density	8.81 (1, 70)	0.0041	0.737 (1, 70)	0.39	0.113	4.40 (2, 69)	0.016	
	adj R² = 0.099		adj R ² = -0.004					
Biomass	1.28 (1, 34)	0.27	0.0424 (1, 34)	0.84	0.363	0.621 (2, 33)	0.54	
Sown Biomass			Unsovn Biomass		MV Biomass			
	F(df)	<i>p</i>	F(df)	<i>p</i>	V	F(df)	<i>p</i>	
JOINT								
site	113 (2, 98)	<0.0001	76.4 (2, 98)	< 0.0001	1.29	88.5 (4, 196)	< 0.0001	
breeding history	0.704 (1, 98)	0.40	0.314 (1, 98)	0.58	0.00894	0.437 (2, 197)	0.65	
foundation number	0.731 (1, 98)	0.39	0.386 (1, 98)	0.54	0.00663	0.324 (2, 197)	0.72	
site x breed.	1.40 (2, 98)	0.25	0.136 (2, 98)	0.87	0.0289	0.719 (4, 196)	0.58	
site x found.	0.251 (2, 98)	0.78	3.46 (2, 98)	0.035	0.0615	1.55 (4, 196)	0.19	
found. x breed.	2.85 (1, 98)	0.094	0.461 (1, 98)	0.50	0.300	1.49 (2, 197)	0.23	
site	112 (2, 72)	<0.0001	67.9 (2, 72)	< 0.0001	1.41	86.3 (4, 144)	< 0.0001	
strain	1.83 (11, 72)	0.064	0.233 (11, 72)	0.99	0.252	0.942 (22, 144)	0.54	
site x strain	1.27 (22, 72)	0.22	0.910 (22, 72)	0.58	0.479	1.03 (44, 144)	0.44	
site	103 (1, 68)	<0.0001	158 (1, 68)	< 0.0001	0.679	70.7 (2, 67)	< 0.0001	
stand density	0.0315 (1, 68)	0.86	0.0035 (1, 68)	0.95	0.00060	0.020 (2, 67)	0.98	
site x stand	1.89 (1, 68)	0.17	3.06 (1, 68)	0.085	0.0576	2.047 (2, 67)	0.14	
site	101 (1, 68)	< 0.0001	150 (1, 68)	< 0.0001	0.716	84.6 (2, 67)	< 0.0001	
biomass	0.328 (1, 68)	0.57	0.123 (1, 68)	0.73	0.00829	0.280 (2, 67)	0.76	
site x biomass	0.822 (1, 68)	0.37	0.462 (1, 68)	0.50	0.0154	0.523 (2, 67)	0.60	
STAPLES								
Breeding history	1.706 (1, 32)	0.20	0.458 (1, 32)	0.50	0.0604	0.996 (2, 31)	0.38	
Foundation-number	0.929 (1, 32)	0.34	4.26 (1, 32)	0.047	0.112	1.96 (2, 31)	0.16	
Breed. x found.	0.378 (1, 32)	0.54	1.36 (1, 32)	0.25	0.054	0.890 (2, 31)	0.42	
Strain	1.07 (11, 24)	0.43	1.28 (11, 24)	0.29	0.699	1.17 (11, 48)	0.31	
Biomass	0.080 (1, 34)	0.78	0.371 (1, 34)	0.55	0.0145	0.243 (2, 33)	0.79	
ST. PAUL								
Breeding history	0.698 (1, 32)	0.41	0.0000 (1, 32)	0.99	0.0218	0.346 (2, 31)	0.71	
Foundation-number	0.002 (1, 32)	0.96	0.672 (1, 32)	0.42	0.0215	0.340 (2, 31)	0.71	

Breed. x found.	0.325 (1, 32)	0.57	0.491 (1, 32)	0.49	0.0217	0.344 (2, 31)	0.71
Strain	0.555 (11, 24)	0.84	0.441 (11, 24)	0.92	0.361	0.480 (22, 48)	0.97
Stand density	0.117 (1, 34)	0.73	1.25 (1, 34)	0.27	0.0362	0.621 (2, 33)	0.54
Biomass	0.151 (1, 34)	0.70	0.607 (1, 34)	0.44	0.0255	0.431 (2, 33)	0.65
WASECA							
Breeding history	0.934 (1, 32)	0.34	0.0469 (1, 32)	0.83	0.0284	0.452 (2, 31)	0.64
Foundation-number	0.314 (1, 32)	0.58	0.671 (1, 32)	0.42	0.0324	0.520 (2, 31)	0.60
Breed. x found.	3.45 (1, 32)	0.072	1.80 (1, 32)	0.19	0.119	2.10 (2, 31)	0.14
Strain	1.07 (11, 24)	0.43	1.28 (11, 24)	0.29	0.699	1.17 (22, 48)	0.31
Stand density	3.69 (1, 70)	0.059	0.0976 (1, 70)	0.76	0.0531	1.93 (2, 69)	0.15
	adj R² = 0.04						
Biomass	0.0804 (1, 34)	0.78	0.371 (1, 34)	0.55	0.0145	0.243 (2, 33)	0.79
Sown Spp. Richness			Unsovn Spp. Richness		MV Spp. Richness		
	F(df)	p	F(df)	p	V	F(df)	p
JOINT							
site	213 (2, 206)	< 0.0001	48.6 (1, 206)	< 0.0001	0.889	82.4 (4, 412)	< 0.0001
breeding history	0.0247 (1, 206)	0.88	0.485 (1, 206)	0.49	0.00539	0.556 (2, 205)	0.57
foundation number	0.0476 (1, 206)	0.83	2.44 (1, 206)	0.12	0.0122	1.267 (2, 205)	0.28
site x breed.	0.182 (2, 206)	0.83	1.24 (2, 206)	0.29	0.0112	0.581 (4, 412)	0.68
site x found.	2.35 (2, 206)	0.098	0.459 (2, 206)	0.63	0.0226	1.18 (4, 412)	0.32
found. x breed.	0.241 (1, 206)	0.62	0.353 (1, 68)	0.55	0.00218	0.224 (2, 205)	0.80
site	228 (2, 180)	< 0.0001	53.0 (2, 180)	< 0.0001	0.974	85.5 (4, 360)	< 0.0001
strain	0.333 (11, 180)	0.98	2.74 (11, 180)	0.0026	0.187	1.69 (22, 360)	0.028
site x strain	0.745 (22, 180)	0.79	0.990 (22, 180)	0.48	0.184	0.829 (44, 360)	0.77
site	214 (2, 210)	< 0.0001	48.5 (2, 210)	< 0.0001	0.828	74.1 (4, 420)	< 0.0001
stand density	1.03 (1, 210)	0.31	0.876 (1, 210)	0.35	0.0136	1.44 (2, 209)	0.24
site x stand	0.572 (2, 210)	0.57	0.660 (2, 210)	0.52	0.00959	0.506 (4, 420)	0.73
site	0.247 (1, 68)	0.62	7.36 (1, 68)	0.0084	0.0893	3.28 (2, 67)	0.44
biomass	0.00570 (1, 68)	0.94	0.0209 (1, 68)	0.88	0.000471	0.0158 (2, 67)	0.98
site x biomass	1.20 (1, 68)	0.28	0.0490 (1, 68)	0.83	0.0173	0.590 (2, 67)	0.55
MORRIS							
Breeding history	0.0271 (1, 68)	0.87	0.141 (1, 68)	0.71	0.00347	0.117 (2, 67)	0.89
Foundation-number	0.518 (1, 68)	0.47	1.56 (1, 68)	0.22	0.024	0.816 (2, 67)	0.45
Breed. x found.	0.278 (1, 68)	0.60	0.028 (1, 68)	0.87	0.00408	0.137 (2, 67)	0.87
Strain	0.504 (11, 60)	0.89	0.629 (11, 60)	0.80	0.228	0.701 (2, 22)	0.83

Stand density	0.260 (1, 70)	0.61	0.591 (1, 70)	0.44	0.00914	402 (2, 69)	< 0.0001
ST. PAUL							
Breeding history	0.0820 (1, 68)	0.78	0.878	0.35	0.0191	0.652 (2, 67)	0.52
Foundation-number	0.825 (1, 68)	0.36	3.02	0.087	0.0494	1.74 (2, 67)	0.18
Breed. x found.	2.24 (1, 68)	0.14	0.295	0.59	0.050	1.76 (2, 67)	0.18
Strain	1.17 (11, 60)	0.32	1.99 (11, 60)	0.046	0.405	1.39 (22, 120)	0.13
Stand density	0.651 (1, 70)	0.42	0.424 (1, 70)	0.52	0.023	0.820 (2, 69)	0.44
Biomass	0.0125 (1, 34)	0.91	0.0417	0.16	0.0630	1.11 (2, 33)	0.34
WASECA							
Breeding history	0.185 (1, 68)	0.67	1.68 (1, 68)	0.20	0.0265	0.909 (2, 67)	0.41
Foundation-number	5.54 (1, 68)	0.021	0.0659 (1, 68)	0.80	0.0777	2.82 (2, 67)	0.066
Breed. x found.	0.113 (1, 68)	0.74	1.45 (1, 68)	0.23	0.0226	0.776 (2, 67)	0.46
Strain	0.742 (11, 60)	0.69	0.658 (11, 60)	0.78	0.423	1.46 (22, 120)	0.10
Stand density	3.69 (1, 70)	0.059	0.0976 (1, 70)	0.76	0.0531	1.93 (2, 69)	0.15
Biomass	0.0572 (1, 34)	0.81	0.184 (1, 34)	0.67	0.00700	0.116 (2, 33)	0.89
		Sown HB			Unsown HB	MV HB	
		F(df)	p	F(df)	p	V	p
JOINT							
site	342 (2, 203)	< 0.0001	62.4 (2, 203)	< 0.0001	1.11	127 (4, 406)	< 0.0001
breeding history	0.172 (1, 203)	0.68	0.60 (1, 203)	0.44	0.00354	0.359 (2, 202)	0.70
foundation number	0.698 (1, 203)	0.40	0.0263 (1, 203)	0.87	0.00415	0.421 (2, 202)	0.66
site x breed.	0.349 (2, 203)	0.71	0.713 (2, 203)	0.49	0.0110	0.563 (4, 406)	0.69
site x found.	1.15 (2, 203)	0.32	0.0786 (2, 203)	0.92	0.0142	0.727 (4, 406)	0.57
found. x breed.	0.0080 (1, 203)	0.93	0.0364 (1, 203)	0.85	0.00023	0.023 (2, 202)	0.98
site	339 (2, 177)	< 0.0001	63.2 (2, 177)	< 0.0001	1.17	124 (4, 354)	< 0.0001
strain	0.575 (11, 177)	0.85	1.33 (11, 177)	0.21	0.108	0.922 (22, 354)	0.57
site x strain	0.976 (22, 177)	0.50	0.735 (22, 177)	0.80	0.193	0.860 (44, 354)	0.72
site	294 (2, 207)	< 0.0001	64.6 (2, 207)	< 0.0001	1.00	104 (4, 414)	< 0.0001
stand density	1.12 (1, 207)	0.29	1.72 (1, 207)	0.19	0.0131	1.37 (2, 206)	0.26
site x stand	0.151 (2, 207)	0.86	1.75 (2, 207)	0.18	0.0183	0.953 (4, 414)	0.43
site	5.40 (1, 68)	0.00021	49.6 (1, 68)	< 0.0001	0.432	25.5 (2, 67)	< 0.0001
biomass	0.293 (1, 68)	0.59	0.0769 (1, 68)	0.78	0.00494	0.166 (2, 67)	0.85
site x biomass	1.09 (1, 68)	0.30	0.140 (1, 68)	0.71	0.0166	0.566 (2, 67)	0.57
MORRIS							
Breeding history	0.120 (1, 65)	0.73	1.82 (1, 65)	0.18	0.0307	1.01 (2, 64)	0.37

Foundation-number	0.0173 (1, 65)	0.90	0.0276 (1, 65)	0.87	0.000767	0.0246 (2, 64)	0.98
Breed. x found.	0.503 (1, 65)	0.48	1.89 (1, 65)	0.17	0.0388	1.29 (2, 64)	0.28
Strain	0.985 (11, 57)	0.47	0.920 (11, 57)	0.53	0.302	114 (22, 114)	0.57
Stand density	3.09 (1, 67)	0.083	4.58 (1, 67)	0.036	0.100	3.68 (2, 66)	0.031
	<i>adj R²: 0.03</i>		<i>adj R²: 0.05</i>				
ST. PAUL							
Breeding history	0.0201 (1, 68)	0.47	0.239 (1, 68)	0.63	0.0118	0.40 (2, 67)	0.67
Foundation-number	0.0201 (1, 68)	0.89	0.104 (1, 68)	0.75	0.00234	0.079 (2, 67)	0.92
Breed. x found.	0.391 (1, 68)	0.53	0.123 (1, 68)	0.73	0.00786	0.265 (2, 67)	0.77
Strain	0.661 (11, 60)	0.77	0.783 (11, 60)	0.66	0.231	0.712 (22, 120)	0.82
Stand density	0.895 (1, 70)	0.35	0.994 (1, 70)	0.32	0.0277	0.983	0.38
Biomass	0.536 (1, 34)	0.47	0.102 (1, 34)	0.75	0.0192	0.323 (2, 33)	0.73
WASECA							
Breeding history	0.463 (1, 68)	0.50	0.171 (1, 68)	0.68	0.0115	0.388 (2, 67)	0.68
Foundation-number	4.70 (1, 68)	0.034	0.0443 (1, 68)	0.83	0.0769	2.79 (2, 67)	0.069
Breed. x found.	0.0890 (1, 68)	0.77	1.67 (1, 68)	0.20	0.0287	0.990 (2, 67)	0.38
Strain	0.642 (11, 60)	0.79	1.12 (11, 60)	0.36	0.289	0.921 (22, 120)	0.57
Stand density	1.59 (11, 58)	0.127	0.883 (11, 58)	0.56	0.377	1.23 (22, 116)	0.24
Biomass	0.851 (1, 34)	0.36	0.117 (1, 34)	0.73	0.0244	0.413 (2, 33)	0.66
Sown HBE			Unsown HBE		MV HBE		
	F(df)	p	F(df)	p	V	F(df)	p
JOINT							
site	63.6 (2, 191)	< 0.0001	68.4 (2, 191)	< 0.0001	0.617	42.6 (4, 382)	< 0.0001
breeding history	0.107 (1, 191)	0.74	1.69 (1, 191)	0.20	0.00912	0.874 (2, 190)	0.42
foundation number	0.449 (1, 191)	0.50	0.184 (1, 191)	0.67	0.00444	0.423 (2, 190)	0.66
site x breed.	0.167 (2, 191)	0.85	1.42 (2, 191)	0.24	0.0178	0.855 (4, 382)	0.49
site x found.	0.949 (2, 191)	0.39	0.00260 (2, 191)	0.99	0.00893	0.428 (4, 382)	0.79
found. x breed.	3.22 (1, 191)	0.074	0.00660 (1, 191)	0.94	0.0167	1.62 (2, 190)	0.20
site	72.4 (2, 165)	< 0.0001	66.2 (2, 165)	< 0.0001	0.673	41.8 (4, 330)	< 0.0001
strain	1.30 (11, 165)	0.23	0.938 (11, 165)	0.51	0.140	1.13 (22, 330)	0.31
site x strain	2.05 (22, 165)	0.0059	0.638 (22, 165)	0.89	0.295	1.30 (44, 330)	0.11
site	53.2 (2, 194)	< 0.0001	68.0 (2, 194)	< 0.0001	0.533	35.3 (4, 388)	< 0.0001
stand density	0.253 (1, 194)	0.62	0.0000 (1, 194)	0.99	0.00131	0.126 (2, 193)	0.88
site x stand	0.0623 (2, 194)	0.94	1.18 (2, 194)	0.31	0.0128	0.623 (4, 388)	0.65
site	0.670 (1, 66)	0.42	9.42 (1, 66)	0.0031	0.130	4.85 (2, 65)	0.011

	biomass	0.694 (1, 66)	0.41	0.00280 (1, 66)	0.96	0.0107	0.350 (2, 65)	0.71
	site x biomass	1.35 (1, 66)	0.25	0.459 (1, 66)	0.50	0.029	0.972 (2, 65)	0.48
MORRIS								
	Breeding history	0.367 (1, 55)	0.55	0.545 (1, 55)	0.46	0.0143	0.391 (2, 54)	0.68
	Foundation-number	0.57 (1, 55)	0.45	0.0208 (1, 55)	0.87	0.0110	0.270 (2, 54)	0.74
	Breed. x found.	3.40 (1, 55)	0.071	1.55 (1, 55)	0.22	0.0893	2.65 (2, 54)	0.080
	Strain	2.59 (11, 47)	0.012	0.660 (11, 47)	0.77	0.517	1.49 (22, 94)	0.097
	Stand density	0.00730 (1, 56)	0.93	2.33 (1, 56)	0.13	0.0399	1.14 (2, 55)	0.33
ST. PAUL								
	Breeding history	0.000300 (1, 68)	0.99	1.01 (1, 68)	0.32	0.0146	0.50 (2, 67)	0.61
	Foundation-number	0.768 (1, 68)	0.38	0.163 (1, 68)	0.69	0.0153	0.53 (2, 67)	0.60
	Breed. x found.	0.116 (1, 68)	0.73	0.0131 (1, 68)	0.91	0.00191	0.0641 (2, 67)	0.94
	Strain	0.320 (11, 60)	0.98	0.494 (11, 60)	0.90	0.140	0.411 (22, 120)	0.99
	Stand density	0.154 (1, 70)	0.70	0.371 (0.54)	1, 70	0.00762	0.265 (2, 69)	0.77
	Biomass	0.942 (1, 34)	0.34	0.0547 (1, 34)	0.82	0.0334	0.571 (2, 33)	0.57
WASECA								
	Breeding history	0.00180 (1, 66)	0.97	2.07 (1, 66)	0.15	0.0311	1.04 (2, 65)	0.36
	Foundation-number	0.890 (1, 66)	0.35	0.0282 (1, 66)	0.87	0.0141	0.465 (2, 65)	0.63
	Breed. x found.	0.427 (1, 66)	0.52	0.223 (1, 66)	0.64	0.00876	0.287 (2, 65)	0.75
	Strain	1.28 (11, 58)	0.26	0.883 (11, 58)	0.56	0.344	1.10 (22, 116)	0.36
	Stand density	0.489 (1, 68)	0.49	0.447 (1, 68)	0.51	0.0163	0.557 (2, 67)	0.58
	Biomass	1.15 (1, 32)	0.29	0.308 (1, 32)	0.58	0.0426	0.690 (2, 31)	0.51

Table 2- 5: Results of UV and MV ANOVAs testing the effects of switchgrass population characteristics and performance on native and exotic community metrics. Joint-site biomass analyses include data from Staples, St. Paul, Waseca; all other joint analyses include data from Morris, St. Paul, Waseca. Bold text: $p < 0.05$. Bold italicized text: $p < 0.1$.

	Native Abundance		Exotic Abundance		MV Abundance		
	F(df)	<i>p</i>	F(df)	<i>p</i>	V	F(df)	<i>P</i>
JOINT							
site	30.8 (2, 206)	< 0.0001	113 (2, 206)	< 0.0001	0.612	45.4 (4, 412)	< 0.0001
breeding history	0.601 (1, 206)	0.44	0.333 (1, 206)	0.56	0.00511	0.527 (2, 205)	0.59
foundation number	0.161 (1, 206)	0.69	0.534 (1, 206)	0.46	0.00247	0.254 (2, 205)	0.78

site x breed.	0.0521 (2, 206)	0.95	2.14 (2, 206)	0.12	0.0206	1.07 (4, 412)	0.37
site x found.	1.35 (2, 206)	0.26	0.683 (2, 206)	0.51	0.0174	0.905 (4, 412)	0.46
found. x breed.	0.113 (1, 206)	0.74	0.0735 (1, 206)	0.79	0.00081	0.083 (2, 205)	0.92
site	29.8 (2, 180)	< 0.0001	127 (2, 180)	< 0.0001	0.665	44.8 (4, 360)	< 0.0001
strain	0.729 (11, 180)	0.71	1.64 (11, 180)	0.091	0.130	1.14 (22, 360)	0.30
site x strain	0.686 (22, 180)	0.85	1.84 (22, 180)	0.016	0.266	1.25 (44, 360)	0.14
site	24.9 (2, 210)	< 0.0001	114 (2, 210)	< 0.0001	0.580	42.9 (4, 420)	< 0.0001
stand density	1.57 (1, 210)	0.21	1.26 (1, 210)	0.26	0.0153	1.63 (2, 209)	0.20
site x stand	1.13 (2, 210)	0.33	1.54 (2, 210)	0.22	0.0231	1.23 (4, 420)	0.30
site	15.9 (1, 68)	0.00017	4.98 (1, 68)	0.029	0.280	13.0 (2, 67)	< 0.0001
biomass	0.457 (1, 68)	0.50	0.00390 (1, 68)	0.95	0.00700	0.236 (2, 67)	0.79
site x biomass	0.0266 (1, 68)	0.87	0.181 (1, 68)	0.67	0.00268	0.0899 (2, 67)	0.91
MORRIS							
Breeding history	0.0765 (1, 68)	0.78	0.987 (1, 68)	0.32	0.0173	0.590 (2, 67)	0.56
Foundation-number	0.199 (1, 68)	0.66	0.816 (1, 68)	0.37	0.0131	0.440 (2, 67)	0.64
Breed. x found.	0.0238 (1, 68)	0.88	0.939 (1, 68)	0.34	0.0136	0.460 (2, 67)	0.63
Strain	0.263 (11, 60)	0.99	1.59 (11, 60)	0.125	0.0264	0.83 (22, 120)	0.689
Stand density	1.044 (1, 70)	0.31	0.0404 (1, 70)	0.841	0.0147	0.51 (2, 69)	0.60
ST. PAUL							
Breeding history	0.0952 (1, 68)	0.76	7.21 (1, 68)	0.0091	0.0967	3.59 (2, 67)	0.033
Foundation-number	2.74 (1, 68)	0.10	1.71 (1, 68)	0.20	0.0442	1.55 (2, 67)	0.22
Breed. x found.	0.0849 (1, 68)	0.77	0.0694 (1, 68)	0.79	0.00222	0.0748 (2, 67)	0.93
Strain	0.714 (11, 60)	0.72	1.66 (11, 60)	0.10	0.343	1.13 (22, 120)	0.33
Stand density	0.722 (1, 70)	0.40	5.029 (1, 70)	0.028	0.0778	2.91 (2, 69)	0.061
Biomass	0.36 (1, 34)	0.55	0.0009 (1, 34)	0.98	0.0107	0.179 (2, 33)	0.84
WASECA							
Breeding history	0.415 (1, 68)	0.52	0.170 (1, 68)	0.68	0.0161	0.547 (2, 67)	0.58
Foundation-number	1.92 (1, 68)	0.17	0.165 (1, 68)	0.69	0.0337	1.17 (2, 67)	0.32
Breed. x found.	1.34 (1, 68)	0.25	0.0146 (1, 68)	0.90	0.0280	0.966 (2, 67)	0.39
Strain	0.875 (11, 60)	0.57	1.63 (11, 60)	0.11	0.349	1.15 (22, 120)	0.30
Stand density	4.85 (1, 70)	0.031	0.682 (1, 70)	0.41	0.677	2.50 (2, 69)	0.089
	adj R² = 0.05						
Biomass	0.0956 (1, 34)	0.76	0.132 (1, 34)	0.72	0.00453	0.0751 (2, 33)	0.93

	Native Biomass		Exotic Biomass		V	MV Biomass	
	F(df)	<i>p</i>	F(df)	<i>p</i>		F(df)	<i>p</i>
JOINT							
site	72.1 (2, 98)	< 0.0001	73.2 (2, 98)	< 0.0001	1.20	72.9 (4, 196)	< 0.0001
breeding history	0.697 (1, 98)	0.406	0.817 (1, 98)	0.37	0.0136	0.700 (2, 97)	0.52
foundation number	0.00340 (1, 98)	0.95	1.17 (1, 98)	0.28	0.0118	0.600 (2, 97)	0.56
site x breed.	1.95 (2, 98)	0.15	1.22 (2, 98)	0.30	0.0652	1.700 (4, 196)	0.16
site x found.	1.10 (2, 98)	0.34	2.86 (2, 98)	0.062	0.0703	1.800 (4, 106)	0.13
found. x breed.	0.0631 (1, 98)	0.80	1.06 (1, 98)	0.31	0.0122	0.600 (2, 97)	0.55
site	64.6 (2, 72)	< 0.0001	76.4 (2, 72)	< 0.0001	1.32	70.3 (4, 144)	< 0.0001
strain	0.518 (11, 72)	0.89	0.718 (11, 72)	0.72	0.179	0.643 (22, 144)	0.89
site x strain	0.785 (22, 72)	0.73	1.57 (22, 72)	0.079	0.508	1.11 (44, 144)	0.31
site	15.8 (1, 68)	0.0002	166 (1, 68)	< 0.0001	0.643	60.4 (2, 67)	< 0.0001
stand density	0.0334 (1, 68)	0.86	0.640 (1, 68)	0.43	0.0107	0.362 (2, 67)	0.70
site x stand	0.619 (1, 68)	0.43	1.13 (1, 68)	0.29	0.292	1.01 (2, 67)	0.37
site	65.2 (2, 102)	< 0.0001	69.0 (2, 102)	< 0.0001	1.10	61.9 (4, 204)	< 0.0001
biomass	0.264 (1, 102)	0.61	0.181 (1, 102)	0.67	0.00496	0.252 (2, 101)	0.78
site x biomass	0.202 (2, 102)	0.82	0.641 (2, 102)	0.53	0.0183	0.470 (4, 204)	0.76
STAPLES							
Breeding history	1.91 (1, 32)	0.18	0.407 (1, 32)	0.53	0.0651	1.08 (2, 31)	0.35
Foundation-number	1.15 (1, 32)	0.29	5.15 (1, 32)	0.030	0.136	2.44 (2, 31)	0.10
Breed. x found.	0.476 (1, 32)	0.50	1.54 (1, 32)	0.22	0.0619	1.02 (2, 31)	0.37
Strain	0.995 (11, 24)	0.48	1.96 (11, 24)	0.081	0.790	1.42 (22, 48)	0.15
Biomass	0.086 (1, 34)	0.77	0.0161 (1, 34)	0.90	0.00318	0.0526 (2, 33)	0.95
ST. PAUL							
Breeding history	2.59 (1, 32)	0.12	0.7113 (1, 32)	0.41	0.0776	1.30 (2, 31)	0.29
Foundation-number	1.43 (1, 32)	0.24	10.8 (1, 32)	0.0025	0.230	4.63 (2, 31)	0.017
Breed. x found.	0.657 (1, 32)	0.42	5.85 (1, 32)	0.021	0.155	2.83 (2, 31)	0.074
Strain	0.448 (11, 24)	0.92	2.54 (11, 24)	0.027	0.646	1.04 (22, 48)	0.44
Stand density	0.00940 (1, 34)	0.92	0.836 (1, 34)	0.37	0.0263	0.445 (2, 33)	0.64
Biomass	0.0677 (1, 34)	0.80	0.158 (1, 34)	0.69	0.0106	0.176 (2, 33)	0.84
WASECA							
Breeding history	0.542 (1, 32)	0.47	1.99 (1, 32)	0.17	0.0807	1.36 (2, 32)	0.27
Foundation-number	0.462 (1, 32)	0.50	0.0014 (1, 32)	0.97	0.0106	0.166 (2, 31)	0.85
Breed. x found.	3.13 (1, 32)	0.086	0.0315 (1, 32)	0.86	0.0892	1.52 (2, 31)	0.23

	Strain	1.18 (11, 24)	0.35	0.955 (11, 24)	0.510	0.662	1.08 (22, 48)	0.40
	Stand density	1.18 (1, 34)	0.28	0.890 (1, 34)	0.35	0.0645	1.14 (2, 33)	0.33
	Biomass	0.735 (1, 34)	0.40	0.880 (1, 34)	0.35	0.0507	0.881 (2, 33)	0.42
	Native Spp. Richness			Exotic Spp. Richness		MV Spp. Richness		
		F(df)	p	F(df)	p	V	F(df)	p
JOINT								
	site	40.6 (2, 206)	< 0.0001	79.8 (2, 206)	< 0.0001	0.720	58.0 (4, 412)	< 0.0001
	breeding history	0.0415 (1, 206)	0.84	4.48 (1, 206)	0.035	0.0226	2.37 (2, 205)	0.096
	foundation number	0.588 (1, 206)	0.44	0.00380 (1, 206)	0.95	0.00300	0.308 (2, 205)	0.74
	site x breed.	0.0100 (2, 206)	0.99	0.0587 (2, 206)	0.94	0.00064	0.0330 (4, 412)	0.99
	site x found.	3.30 (2, 206)	0.039	0.634 (2, 206)	0.53	0.0323	1.69 (4, 412)	0.15
	found. x breed.	0.224 (1, 206)	0.64	0.664 (1, 206)	0.42	0.00382	0.393 (2, 205)	0.68
	site	40.5 (2, 180)	< 0.0001	88.0 (2, 180)	< 0.0001	0.803	60.4 (4, 360)	< 0.0001
	strain	1.15 (11, 180)	0.33	2.11 (11, 180)	0.021	0.187	1.69 (22, 360)	0.029
	site x strain	0.926 (22, 180)	0.56	1.41 (22, 180)	0.11	0.241	1.12 (44, 360)	0.29
	site	30.2 (2, 210)	< 0.0001	79.8 (2, 210)	< 0.0001	0.562	41.0 (4, 420)	< 0.0001
	stand density	1.13 (1, 210)	0.29	1.11 (1, 210)	0.29	0.0124	1.31 (2, 209)	0.27
	site x stand	1.14 (2, 210)	0.32	0.669 (2, 210)	0.51	0.0166	0.879 (4, 420)	0.48
	site	9.78 (1, 68)	0.0026	61.6 (1, 68)	< 0.0001	0.476	30.5 (2, 67)	< 0.0001
	biomass	0.819 (1, 68)	0.37	0.0562 (1, 68)	0.81	0.0126	0.426 (2, 67)	0.65
	site x biomass	0.561 (1, 68)	0.46	0.106 (1, 68)	0.75	0.00954	0.323 (2, 67)	0.73
MORRIS								
	Breeding history	0.708 (1, 68)	0.40	2.20 (1, 68)	0.14	0.0679	2.44 (2, 67)	0.094
	Foundation-number	0.507 (1, 68)	0.48	1.89 (1, 68)	0.17	0.0277	0.955 (2, 67)	0.39
	Breed. x found.	0.409 (1, 68)	0.52	0.115 (1, 68)	0.74	0.0116	0.392 (2, 67)	0.68
	Strain	0.557 (11, 60)	0.86	0.883 (11, 60)	0.56	0.285	0.907 (22, 120)	0.59
	Stand density	0.833 (1, 70)	0.36	0.154 (1, 70)	0.70	0.0118	0.410 (2, 69)	0.66
ST. PAUL								
	Breeding history	0.0258 (1, 68)	0.87	2.33 (1, 68)	0.13	0.0342	1.19 (2, 67)	0.31
	Foundation-number	1.50 (1, 68)	0.22	0.00300 (1, 68)	0.96	0.0207	0.709 (2, 67)	0.50
	Breed. x found.	0.414 (1, 68)	0.52	0.0452 (1, 68)	0.83	0.00642	0.217 (2, 67)	0.81
	Strain	1.56 (11, 60)	0.13	1.66 (11, 60)	0.10	0.452	1.59 (22, 120)	0.059
	Stand density	0.225 (1, 70)	0.64	4.39 (1, 70)	0.040	0.0651	2.40 (2, 69)	0.098
				adj R² = - 0.01				
	Biomass	0.731 (1, 34)	0.40	0.315 (1, 34)	0.58	0.0318	0.541 (2, 33)	0.59

WASECA							
Breeding history	0.00001 (1, 68)	0.99	0.880 (1, 68)	0.35	0.0128	0.434 (2, 67)	0.65
Foundation-number	3.17 (1, 68)	0.079	0.560 (1, 68)	0.46	0.0492	1.73 (2, 67)	0.18
Breed. x found.	0.444 (1, 68)	0.51	0.372 (1, 68)	0.54	0.0124	0.422 (2, 67)	0.66
Strain	0.669 (11, 60)	0.76	2.13 (11, 60)	0.031	0.401	1.37 (22, 120)	0.14
Stand density	2.04 (1, 70)	0.16	0.351 (1, 70)	0.56	0.0353	1.26 (2, 69)	0.29
Biomass	0.577 (1, 34)	0.45	0.0448 (1, 34)	0.83	0.0172	0.289 (2, 33)	0.75
Native HB			Exotic HB		MV HB		
	F(df)	p	F(df)	p	V	F(df)	p
JOINT							
site	29.6 (2, 198)	< 0.0001	129 (2, 198)	< 0.0001	0.714	55.0 (4, 396)	< 0.0001
breeding history	0.00700 (1, 198)	0.93	1.72 (1, 198)	0.63	0.00864	0.858 (2, 197)	0.43
foundation number	0.176 (1, 198)	0.68	0.236 (1, 198)	0.47	0.00200	0.198 (2, 197)	0.82
site x breed.	0.440 (2, 198)	0.64	0.127 (2, 198)	0.88	0.00573	0.284 (4, 396)	0.89
site x found.	2.34 (2, 198)	0.099	0.387 (2, 198)	0.68	0.0272	1.37 (4, 396)	0.24
found. x breed.	0.0251 (1, 197)	0.87	0.0103 (1, 198)	0.92	0.00018	0.018 (2, 197)	0.98
site	30.3 (2, 172)	< 0.0001	132 (2, 172)	< 0.0001	0.774	54.3 (4, 344)	< 0.0001
strain	1.28 (11, 172)	0.24	0.961 (11, 172)	0.48	0.133	1.12 (22, 344)	0.33
site x strain	0.997 (22, 172)	0.47	1.03 (22, 172)	0.43	0.230	1.02 (22, 344)	0.45
site	15.2 (2, 202)	< 0.0001	132 (2, 202)	< 0.0001	0.546	38.0 (4, 404)	< 0.0001
stand density	0.545 (1, 202)	0.46	2.21 (1, 202)	0.14	0.0132	1.35 (2, 201)	0.26
site x stand	2.36 (2, 202)	0.097	0.342 (2, 202)	0.71	0.0264	1.35 (4, 404)	0.25
site	0.287 (1, 66)	0.59	85.1 (1, 66)	< 0.0001	0.543	38.6 (2, 65)	< 0.0001
biomass	0.867 (1, 66)	0.35	0.931 (1, 66)	0.34	0.0230	0.764 (2, 65)	0.47
site x biomass	0.00272 (1, 66)	0.83	0.00960 (1, 66)	0.92	0.00097	0.0320 (2, 65)	0.97
MORRIS							
Breeding history	0.0263 (1, 66)	0.87	3.24 (1, 66)	0.076	0.0530	1.82 (2, 65)	0.17
Foundation-number	1.24 (1, 66)	0.27	0.734 (1, 66)	0.39	0.0274	0.915 (2, 65)	0.041
Breed. x found.	0.814 (1, 66)	0.37	1.47 (1, 66)	0.23	0.0315	1.06 (2, 65)	0.35
Strain	0.922 (11, 58)	0.53	1.30 (11, 58)	0.25	0.355	1.14 (22, 116)	0.318
Stand density	2.58 (1, 68)	0.11	1.31 (1, 68)	0.26	0.0502	1.77 (2, 67)	0.18
ST. PAUL							
Breeding history	0.0003 (1, 68)	0.99	0.123 (1, 68)	0.73	0.00182	0.0611 (2, 67)	0.94
Foundation-number	0.141 (1, 68)	0.71	0.472 (1, 68)	0.49	0.00720	0.0.243 (2, 67)	0.79
Breed. x found.	0.196 (1, 68)	0.66	0.172 (1, 68)	0.68	0.00507	0.171 (2, 67)	0.84

	Strain	1.26 (11, 60)	0.27	0.100 (11, 60)	0.46	0.342	1.12 (22, 120)	0.33
	Stand density	0.559 (1, 70)	0.46	2.12 (1, 70)	0.15	0.0350	1.25 (2, 69)	0.29
	Biomass	0.847 (1, 34)	0.36	0.786 (1, 34)	0.38	0.0417	0.718 (2, 33)	0.50
WASECA								
	Breeding history	0.481 (1, 62)	0.49	0.638 (1, 62)	0.43	0.0161	0.499 (2, 61)	0.61
	Foundation-number	2.02 (1, 62)	0.16	0.52 (1, 62)	0.47	0.0441	1.41 (2, 61)	0.25
	Breed. x found.	0.796 (1, 62)	0.38	2.20 (1, 62)	0.14	0.0507	1.63 (2, 61)	0.20
	Strain	1.28 (11, 54)	0.26	0.970 (11, 54)	0.48	0.376	1.14 (22, 108)	0.32
	Stand density	0.741 (1, 64)	0.39	0.00150 (1, 64)	0.97	0.115	0.366 (2, 63)	0.70
	Biomass	0.00005 (1, 32)	0.98	0.0919 (1, 32)	0.76	0.00321	0.0498 (2, 31)	0.95
Native HBE				Exotic HBE			MV HBE	
		F(df)	p	F(df)	p	V	F(df)	p
JOINT								
	site	10.1 (2, 178)	< 0.0001	93.9 (2, 178)	< 0.0001	0.619	39.9 (4, 356)	< 0.0001
	breeding history	0.0706 (1, 178)	0.40	0.0490 (1, 178)	0.83	0.00473	0.421 (2, 177)	0.66
	foundation number	0.00170 (1, 178)	0.97	0.0505 (1, 178)	0.82	0.000220	0.019 (2, 177)	0.98
	site x breed.	1.80 (2, 178)	0.17	0.316 (2, 178)	0.73	0.0241	1.09 (4, 356)	0.36
	site x found.	1.40 (2, 178)	0.25	0.366 (2, 178)	0.69	0.0211	0.950 (4, 356)	0.43
	found. x breed.	1.04 (1, 178)	0.31	3.26 (1, 178)	0.073	0.0220	1.99 (2, 177)	0.14
	site	9.91 (2, 152)	< 0.0001	88.4 (2, 152)	< 0.0001	0.653	36.8 (4, 304)	< 0.0001
	strain	0.843 (11, 152)	0.60	0.714 (11, 152)	0.72	0.105	0.764 (22, 304)	0.769
	site x strain	1.01 (22, 152)	0.45	0.547 (22, 152)	0.95	0.206	0.792 (44, 304)	0.824
	site	8.201 (2, 182)	0.00039	94.2 (2, 182)	< 0.0001	0.513	31.4 (4, 364)	< 0.0001
	stand density	0.281 (1, 182)	0.596	0.00420 (1, 182)	0.95	0.00161	0.146 (2, 181)	0.864
	site x stand	0.297 (2, 182)	0.74	0.564 (2, 182)	0.57	0.0100	0.46 (4, 364)	0.77
	site	18.4 (1, 56)	< 0.0001	0.284 (1, 56)	0.60	0.0223	7.87 (2, 55)	0.00098
	biomass	0.00120 (1, 56)	0.97	0.153 (1, 56)	0.70	0.00275	0.0757 (2, 55)	0.93
	site x biomass	2.21 (1, 56)	0.14	0.897 (1, 56)	0.35	0.053	1.54 (2, 55)	0.223
MORRIS								
	Breeding history	0.207 (1, 64)	0.65	0.776 (1, 64)	0.38	0.0244	0.788 (2, 63)	0.46
	Foundation-number	1.85 (1, 64)	0.18	0.00450 (1, 64)	0.95	0.0147	0.471 (2, 63)	0.63
	Breed. x found.	0.183 (1, 64)	0.67	4.00 (1, 64)	0.049	0.0622	2.09 (2, 63)	0.132
	Strain	1.06 (11, 56)	0.41	0.918 (11, 56)	0.53	0.326	0.992 (22, 112)	0.48
	Stand density	0.150 (1, 66)	0.70	0.630 (1, 66)	0.43	0.0120	0.394 (2, 65)	0.68

ST. PAUL								
Breeding history	0.479 (1, 68)	0.49	0.199 (1, 68)	0.66	0.00955	0.323 (2, 67)	0.73	
Foundation-number	2.36 (1, 68)	0.13	0.817 (1, 68)	0.37	0.0421	1.47 (2, 67)	0.24	
Breed. x found.	1.16 (1, 68)	0.29	0.177 (1, 68)	0.68	0.0188	0.643 (2, 67)	0.53	
Strain	0.768 (11, 60)	0.67	0.770 (11, 60)	0.67	0.245	0.760 (22, 120)	0.77	
Stand density	0.243 (1, 70)	0.62	0.0904 (1, 70)	0.76	0.00481	0.167 (2, 69)	0.85	
Biomass	0.0428 (1, 34)	0.84	0.0920 (1, 34)	0.76	0.000341	0.0565 (2, 33)	0.95	
WASECA								
Breeding history	2.75 (1, 44)	0.10	0.187 (1, 44)	0.667	0.0692	1.60 (2, 43)	0.21	
Foundation-number	0.134 (1, 44)	0.72	0.0587 (1, 44)	0.81	0.00339	0.731 (2, 43)	0.93	
Breed. x found.	1.10 (1, 44)	0.30	0.661 (1, 44)	0.42	0.0333	0.741 (2, 43)	0.48	
Strain	0.897 (11, 36)	0.55	0.340 (11, 36)	0.97	0.326	0.638 (22, 72)	0.88	
Stand density	0.00270 (1, 46)	0.96	0.312 (1, 46)	0.58	0.00680	0.154 (2, 45)	0.86	
Biomass	1.91 (1, 22)	0.18	0.624 (1, 22)	0.44	0.0944	1.09 (2, 21)	0.35	

Table 2-6: Results of ANOVAs testing the effects of switchgrass population characteristics on switchgrass performance. Joint-site biomass analyses include data from Staples, St. Paul, Waseca; all other joint analyses include data from Morris, St. Paul, Waseca. Bold text: $p < 0.05$. Bold italicized text: $p < 0.1$.

	Establishment (1 st yr)		Establishment (2 nd yr)		Stand density (3 rd yr)		Biomass (absolute)		Biomass (proportional)	
	F (df)	<i>p</i>	F (df)	<i>p</i>	F (df)	<i>p</i>	F (df)	<i>p</i>	F (df)	<i>p</i>
JOINT										
site	53.7 (3, 245)	< 0.0001	84.8 (3, 275)	< 0.0001	194 (2, 206)	< 0.0001	37.2 (2, 98)	< 0.0001	23.6 (2, 98)	< 0.0001
breeding history	45.9 (1, 245)	< 0.0001	39.2 (1, 275)	< 0.0001	18.2 (1, 206)	< 0.0001	22.6 (1, 98)	< 0.0001	21.1 (1, 98)	< 0.0001
foundation-number	0.999 (1, 245)	0.32	2.53 (1, 275)	0.11	0.0005 (1, 206)	0.98	0.186 (1, 98)	0.67	0.421 (1, 98)	0.52
site x breed.	2.92 (3, 245)	0.035	6.238 (3, 275)	0.00041	5.46 (2, 206)	0.0049	0.529 (2, 98)	0.59	1.72 (2, 98)	0.18
site x found.	0.112 (3, 245)	0.95	1.53 (3, 275)	0.21	1.547 (2, 206)	0.22	1.837 (2, 98)	0.17	2.51 (2, 98)	0.087
breed. x found.	0.242 (1, 245)	0.62	0.0769 (1, 275)	0.78	0.0221 (1, 206)	0.88	2.077 (1, 98)	0.15	2.30 (1, 98)	0.13
site	71.6 (3, 210)	< 0.0001	106 (3, 240)	< 0.0001	234 (2, 180)	< 0.0001	50.3 (2, 72)	< 0.0001	38.9 (2, 72)	< 0.0001
strain	9.83 (11, 210)	< 0.0001	7.57 (11, 240)	< 0.0001	5.52 (11, 180)	< 0.0001	5.30 (11, 72)	< 0.0001	5.84 (11, 72)	< 0.0001
site x strain	1.84 (33, 210)	0.006	3.04 (33, 240)	< 0.0001	2.19 (22, 180)	0.0030	2.00 (22, 72)	0.015	3.66 (22, 72)	< 0.0001
MORRIS										
breeding history	6.84 (1, 68)	0.011	1.53 (1, 68)	0.22	0.0081 (1, 68)	0.93	Data not available		Data not available	
foundation-number	0.0633 (1, 68)	0.80	1.94 (1, 68)	0.17	0.351 (1, 68)	0.56				
breed. x found.	0.0628 (1, 68)	0.80	2.18 (1, 68)	0.14	0.120 (1, 68)	0.73				
strain	3.32 (11, 60)	0.001	0.903 (11, 60)	0.46	1.87 (11, 60)	0.062				
STAPLES										
breeding history	21.5 (1, 68)	< 0.0001	9.654 (1, 68)	0.00286	Data not available		19.7 (1, 32)	0.0001	19.2 (1, 32)	0.00012

foundation- number	0.819 (1, 68)	0.37	4.45 (1, 68)	0.039		0.0728 (1, 32)	0.79	0.183 (1, 32)	0.67	
breed. x found.	1.66 (1, 68)	0.202	1.52 (1, 68)	0.22		5.13 (1, 32)	0.030	6.62 (1, 32)	0.015	
strain	4.81 (11, 60)	< 0.0001	4.62 (11, 60)	< 0.0001		4.68 (11, 24)	< 0.001	4.65 (11, 24)	0.00075	
ST. PAUL										
breeding history	12.0 (1, 38)	0.0013	21.6 (1, 68)	< 0.0001	16.5 (1, 68)	< 0.0035	4.30 (1, 32)	0.046	2.47 (1, 32)	0.13
foundation- number	0.292 (1, 38)	0.59	0.135 (1, 68)	0.72	0.836 (1, 68)	0.36	2.48 (1, 32)	0.13	3.19 (1, 32)	0.084
breed. x found.	1.03 (1, 38)	0.32	0.479 (1, 68)	0.49	0.138 (1, 68)	0.71	0.0318 (1, 32)	0.86	0.0748 (1, 32)	0.79
strain	2.59 (11, 30)	0.019	4.62 (11, 60)	< 0.0001	4.35 (11, 60)	< 0.0001	3.67 (11, 24)	0.00048	5.64 (11, 24)	0.00015
WASECA										
breeding history	7.43 (1, 68)	0.0082	7.37 (1, 68)	0.0084	5.08 (1, 68)	0.027	0.286 (1, 32)	0.60	6.63 (1, 32)	0.015
foundation- number	0.318 (1, 68)	0.58	1.24 (1, 68)	0.27	1.37 (1, 68)	0.25	0.324 (1, 32)	0.57	0.852 (1, 32)	0.36
breed. x found.	1.85 (1, 68)	0.18	0.0299 (1, 68)	0.86	0.177 (1, 68)	0.68	0.300 (1, 32)	0.59	0.518 (1, 32)	0.48
strain	3.98 (11, 60)	0.00045	2.82 (11, 60)	0.005	2.63 (11, 60)	0.0082	1.61 (11, 24)	0.16	2.03 (11, 24)	0.072

Table 2-7: Results from Mann-Whitney-Wilcoxon (*W*) tests of interannual comparisons in switchgrass stand densities. 3rd-year count data from Staples are not available. Bold text: $p < 0.05$. Bold italicized text: $p < 0.1$.

	1 st to 2 nd year		2 nd to 3 rd year		1 st to 3 rd year	
	W	<i>p</i>	W	<i>p</i>	W	<i>p</i>
Joint	45356.5	< 0.0001	30711.5	0.797	34205.5	< 0.0001
Morris	3859	< 0.0001	2303.5	0.008	3613	< 0.0001
Staples	2955	0.15				
St. Paul	2186	0.0037	1762	0.0007	<i>1811</i>	<i>0.078</i>
Waseca	3338	0.0032	2710.5	0.603	3402.5	0.00063

Table 2-8: Results of UV and MV ANOVAs testing effects of switchgrass population characteristics on switchgrass persistence. Bold text: $p < 0.05$. Bold italicized text: $p < 0.1$.

	2 nd -1 st year		UV 3 rd - 2 nd year		3 rd - 1 st year		MV		
	F (df)	<i>p</i>	F(df)	<i>p</i>	F (df)	<i>p</i>	V	F(df)	<i>p</i>
JOINT									
site	14.8 (3, 245)	< 0.0001	33.5 (2, 206)	< 0.0001	4.90 (2, 176)	0.0075	0.322	16.9 (4, 352)	< 0.0001
breeding history	9.79 (1, 245)	0.0040	0.474 (1, 206)	0.49	9.86 (1, 176)	0.0015	0.0564	5.23 (2, 175)	0.0062
foundation-number	0.00760 (1, 245)	0.93	0.624 (1, 206)	0.43	1.13 (1, 176)	0.29	0.00717	0.632 (2, 175)	0.53
site x breed.	1.88 (3, 245)	0.13	0.667 (2, 206)	0.52	4.86 (2, 176)	0.007	0.0599	2.72 (4, 352)	0.030
site x found.	2.16 (3, 245)	0.094	0.278 (2, 206)	0.76	2.82 (2, 176)	0.063	0.0317	1.42 (4, 352)	0.23
breed. x found.	0.603 (1, 245)	0.44	0.285 (1, 206)	0.59	0.536 (1, 176)	0.47	0.00326	0.286 (2, 175)	0.751
site	18.4 (1, 210)	< 0.0001	36.8 (2, 180)	< 0.0001	5.88 (2, 150)	0.003	0.405	19.0 (4, 300)	< 0.0001
strain	4.04 (11, 210)	< 0.0001	1.77 (11, 180)	0.063	3.40 (11, 150)	0.00021	0.291	2.32 (22, 300)	0.00088
site x strain	0.261 (33, 210)	0.00037	1.35 (22, 180)	0.14	2.32 (22, 150)	0.0038	0.500	2.27 (44, 300)	< 0.0001
MORRIS									
breeding history	8.00 (1, 68)	0.0062	0.259 (1, 68)	0.61	8.18 (1, 68)	0.0079	0.0109	4.09 (2, 67)	0.021
foundation-number	0.119 (1, 68)	0.73	1.40 (1, 68)	0.24	0.478 (1, 68)	0.49	0.0220	0.754 (2, 67)	0.47
breed. x found.	0.214 (1, 68)	0.65	0.370 (1, 68)	0.55	0.0656 (1, 68)	0.80	0.00839	0.284 (2, 67)	0.75
strain	2.74 (11, 60)	0.0072	2.06 (11, 60)	0.038	2.12 (11, 60)	0.033	0.608	2.38 (22, 120)	0.0015
STAPLES									
breeding history	2.25 (1, 68)	0.14	Data not available		Data not available		Data not available		
foundation-number	1.40 (1, 68)	0.24	Data not available		Data not available		Data not available		
breed. x found.	0.273 (1, 68)	0.60	Data not available		Data not available		Data not available		
strain	3.51 (11, 60)	0.00076	Data not available		Data not available		Data not available		
ST PAUL									
breeding history	3.53 (1, 38)	0.068	0.716 (1, 68)	0.40	5.42 (1, 38)	0.025	0.133	2.83 (2, 37)	0.072
foundation-number	1.53 (1, 38)	0.22	0.446 (1, 68)	0.51	2.12 (1, 38)	0.15	0.0540	1.06 (2, 37)	0.36
breed. x found.	2.34 (1, 38)	0.13	0.891 (1, 68)	0.35	2.25 (1, 38)	0.14	0.0594	1.17 (2, 37)	0.32
strain	1.45 (11, 30)	0.20	1.53 (11, 60)	0.15	1.83 (11, 30)	0.092	0.0727	1.56 (22, 60)	0.080

WASECA									
breeding history	1.68 (1, 68)	0.20	0.132 (1, 68)	0.72	1.45 (1, 68)	0.23	0.0244	0.836 (2, 67)	0.44
foundation- number	0.153 (1, 68)	0.70	0.000 (1, 68)	1.0	0.177 (1, 68)	0.68	0.00263	0.088 (2, 67)	0.92
breed. x found.	1.64 (1, 68)	0.20	0.257 (1, 68)	0.61	1.24 (1, 68)	0.27	0.0236	0.809 (2, 67)	0.45

Figures

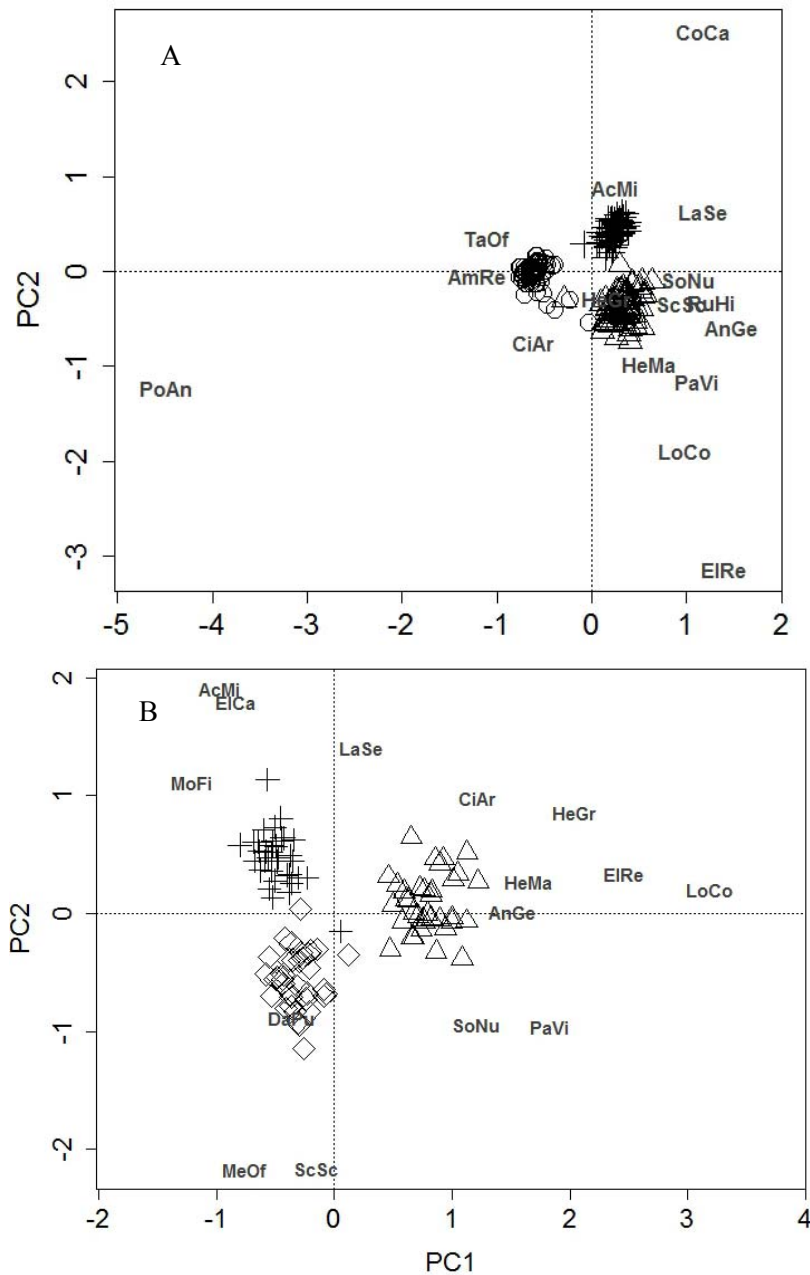


Fig. 2-1: Ordinations of (log) third-year census data (A) and (log) third-year biomass data (B). Circles: Morris, MN. Triangles: St. Paul, MN. Crosses: Waseca, MN. Diamonds: Staples, MN. Not all data are available for all sites. For clarity, only species with $|\text{loadings}| > 0.150$ are shown. Variation explained by the first 2PCs is A: 55%. B: 42%. AcMi: *Achillea millefolium*. AmRe: *Amaranthus retroflexus*. AnGe: *Andropogon gerardii*. CiAr: *Cirsium arvense*. ElCa: *Elymus canadensis*. ElRe: *Elymus repens*. HeGr: *Helianthus grosseserratus*. HeMa: *Helianthus maximiliani*. LaSe: *Lactuca serriola*. LoCo: *Lotus corniculatus*. MeOf: *Melilotus officinalis*. MoFi: *Monarda fistulosa*. PaVi: *Panicum virgatum*. PoAn: *Poa annua*. RuHi: *Rudbeckia hirta*. ScSc: *Schizachyrium scoparium*. SoNu: *Sorghastrum nutans*. TaOf: *Taraxacum officinale*.

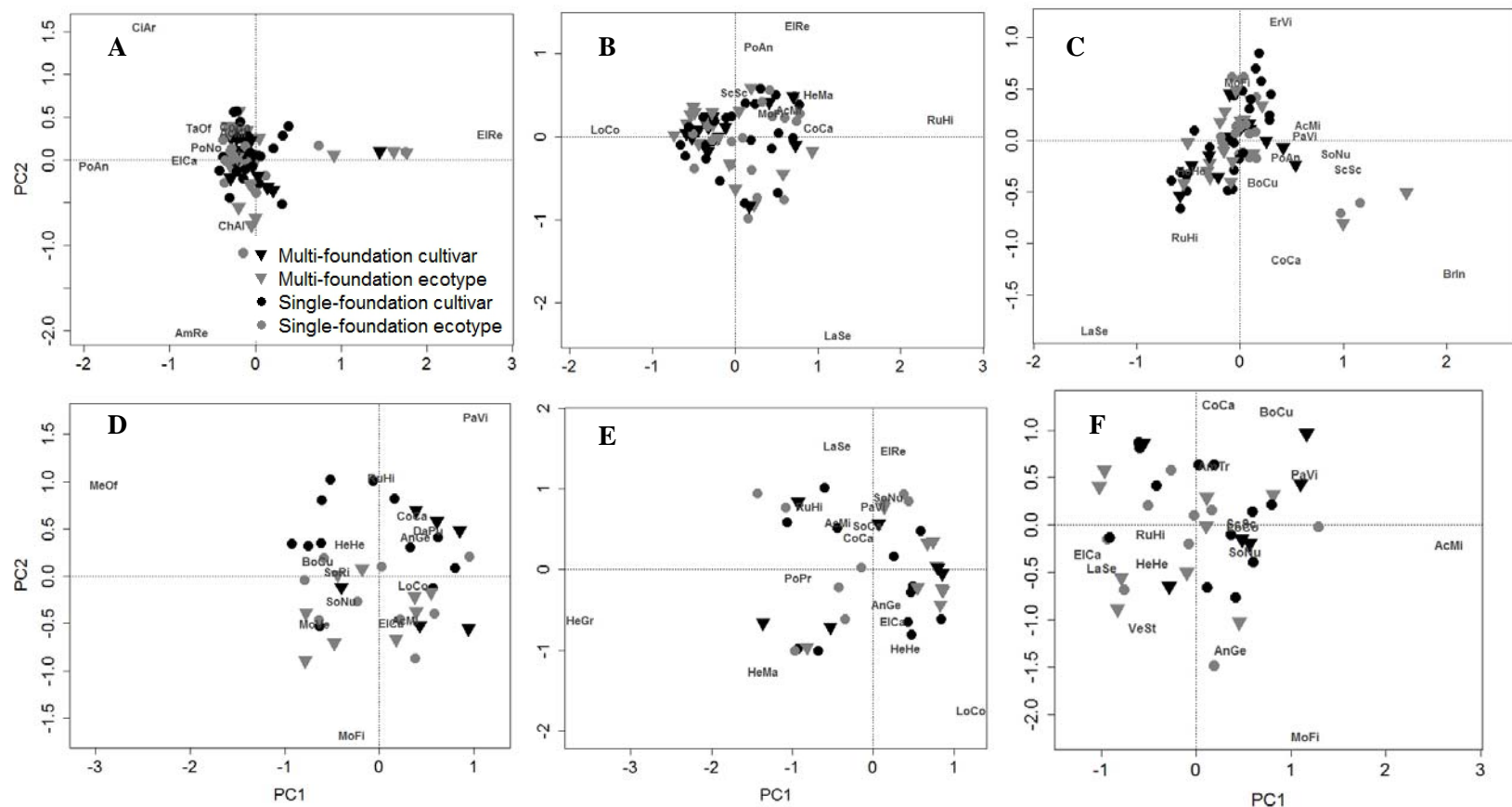


Fig. 2-2: Ordinations of (log) third-year census data from Morris (A), St. Paul (B), and Waseca, MN (C); and of (log) third-year biomass data from Staples (D), St. Paul (E), and Waseca, MN (F). For clarity, only species with $|loadings| > 0.1$ are shown. AcMi: *Achillea millefolium*. AmRe: *Amaranthus retroflexus*. AmTr: *Ambrosia trifida*. AnGe: *Andropogon gerardii*. CiAr: *Cirsium arvense*. ElCa: *Elymus canadensis*. ElRe: *Elymus repens*. HeGr: *Helianthus grosseserratus*. HeMa: *Helianthus maximiliani*. LaSe: *Lactuca serriola*. LoCo: *Lotus corniculatus*. MeOf: *Melilotus officinalis*. MoFi: *Monarda fistulosa*. MoVe: *Mollugo verticillata*. PaVi: *Panicum virgatum*. PoAn: *Poa annua*. PoNo: *Potentilla norvegica*. RuHi: *Rudbeckia hirta*. ScSc: *Schizachyrium scoparium*. SoNu: *Sorghastrum nutans*. SoRi: *Solidago rigida*. TaOf: *Taraxacum officinale*. VeSt: *Verbena stricta*.

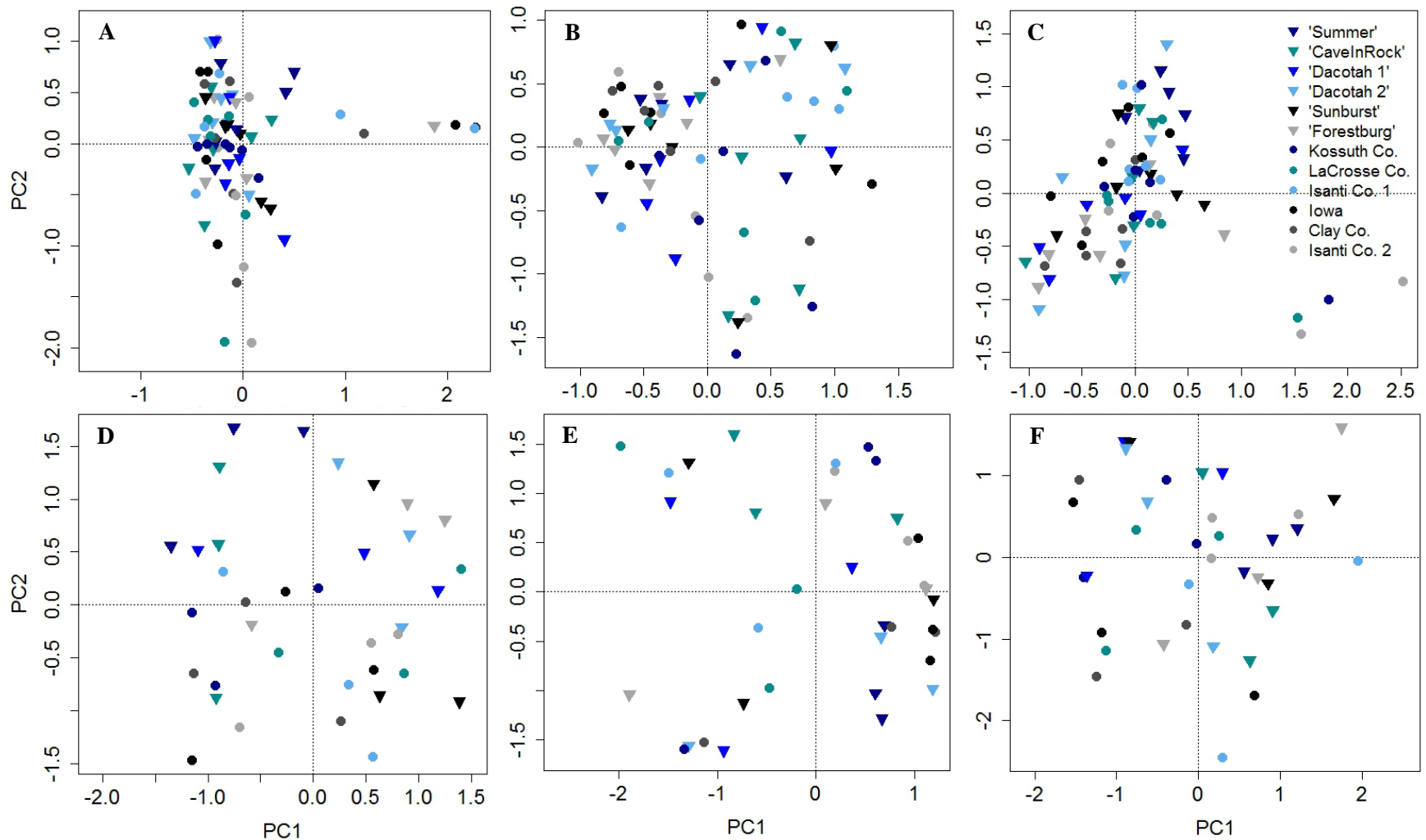


Fig. 2-3: Ordinations of 12 switchgrass stains in species-space based on (log) third-year census data from Morris (A), St. Paul (B), and Waseca, MN (C); and of (log) third-year biomass data from Staples (D), St. Paul (E), and Waseca, MN (F). Triangles: cultivars. Circles: ecotypes. Blue symbols: single-foundation strains. Gray/black symbols: multi-foundation strains.

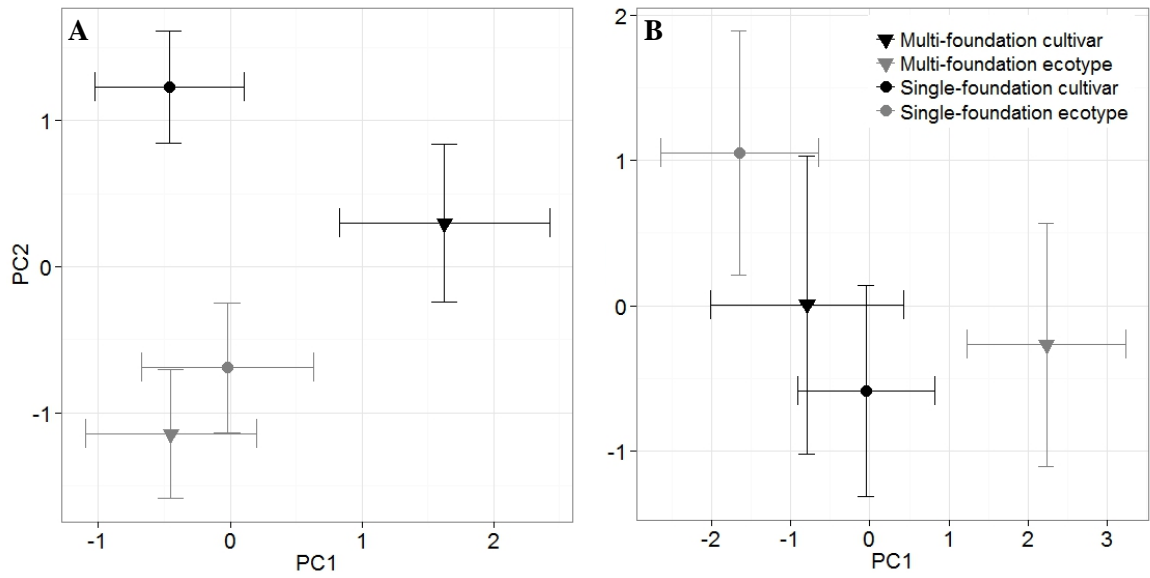


Fig. 2-4: MANOVA-predicted effects (± 1 SE) of switchgrass population characteristics on scores from ordinations of (log) third-year aboveground biomass values from experimental prairies at Staples (A) and St. Paul (B), MN.

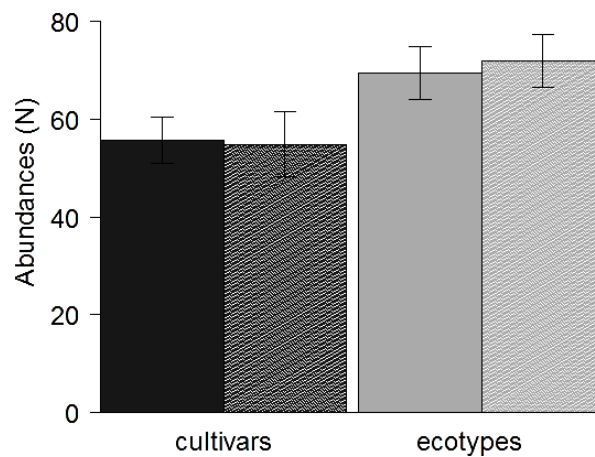


Fig. 2-5: Model-estimated effects (± 1 s.e.) of switchgrass breeding history and foundation-number on third-year plant densities (individuals m^{-2}) in experimental prairies, St. Paul, MN, 2012. Open bars: single-foundation. Hatched bars: multi-foundation. Switchgrass abundance was excluded from calculations.

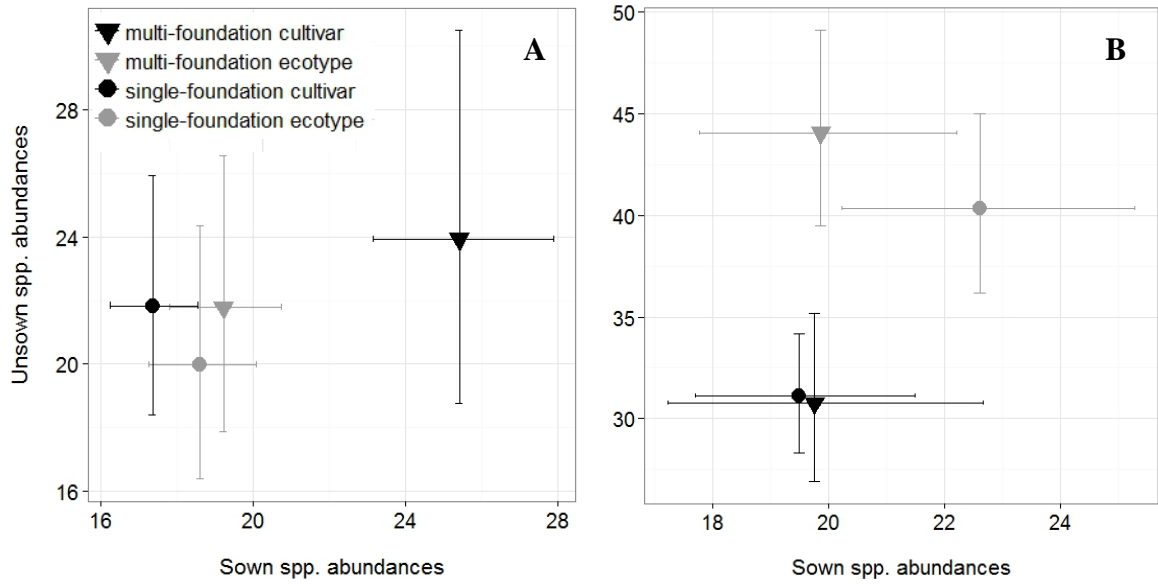


Fig. 2-6: Model-estimated effects (± 1 s.e.) of switchgrass breeding history and foundation-number on third-year abundances of sown or unsown plant species (individuals m^{-2}) in experimental prairies in Waseca (A) and St. Paul (B), Minnesota, 2012. Switchgrass abundances were excluded from calculations.

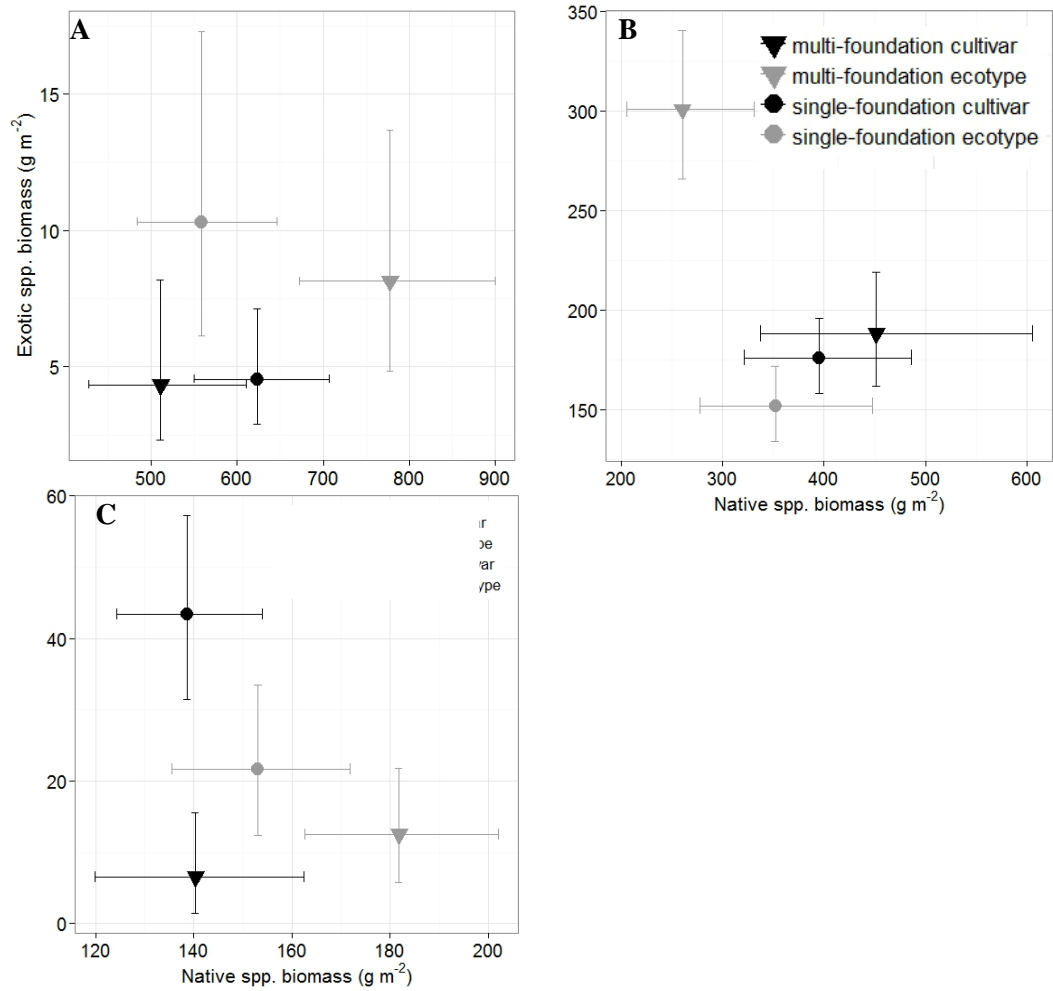


Fig. 2-7: Model-estimated effects (± 1 s.e.) of switchgrass breeding history and foundation-number on third-year aboveground biomass of native and exotic plant species in experimental prairies at Waseca (A), St. Paul (B), and Staples (C), MN, 2012. Switchgrass biomass was excluded from calculations. Note different x- and y-axis scales.

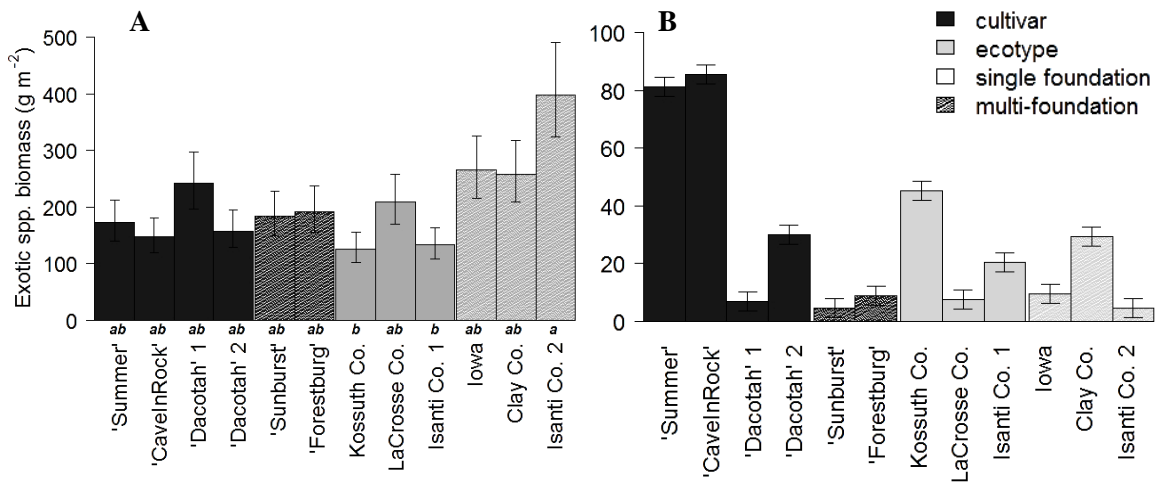


Fig. 2-8: Model-estimated effects (± 1 s.e.) of switchgrass strain on third-year aboveground biomass of exotic plant species in experimental prairies at St. Paul (A) and Staples (B), MN, 2012. Open bars: single-foundation. Hatched bars: multi-foundation. Bars that share lower-case letters are not statistically different based on Student-Newman-Keuls a posteriori tests. No differences were found among switchgrass strains at Staples.

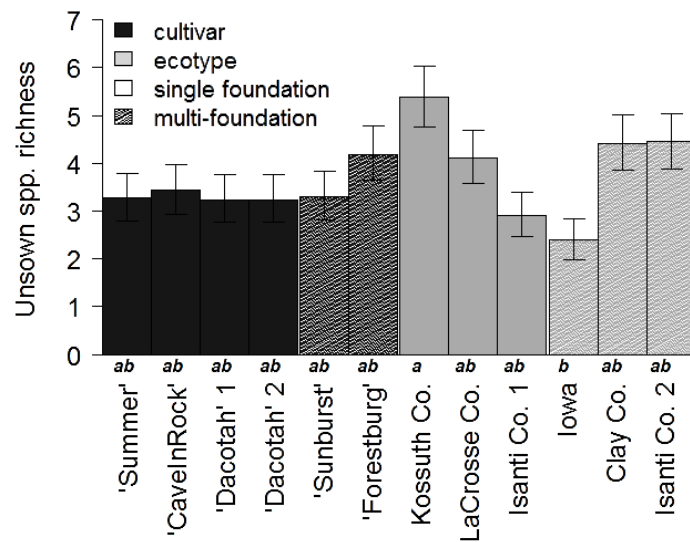


Fig. 2-9: Model-estimated effects (± 1 s.e.) of switchgrass strain on third-year richness of unsown plant species in experimental prairies at Waseca, MN, 2012. Open bars: single-foundation. Hatched bars: multi-foundation. Bars that share lower-case letters are not statistically different based on Student-Newman-Keuls a posteriori tests.

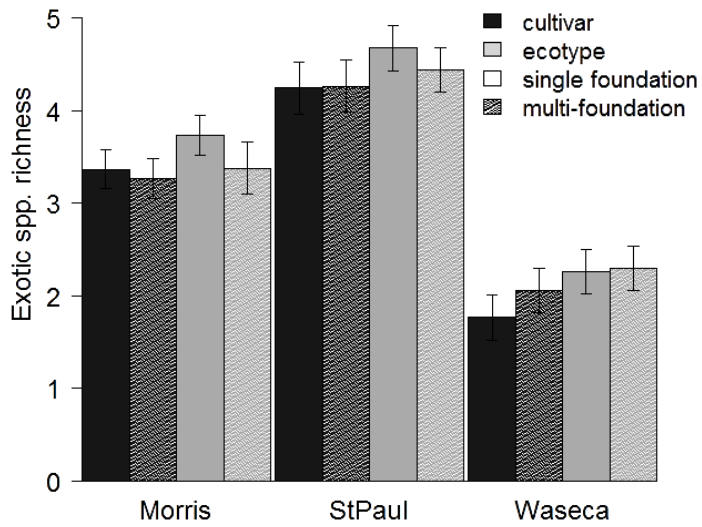


Fig. 2-10: Model-estimated effects (± 1 s.e.) of switchgrass breeding history and foundation-number on third-year richness of exotic species in experimental prairies, analyzed jointly over three sites in Minnesota. Open bars: single-foundation. Hatched bars: multi-foundation.

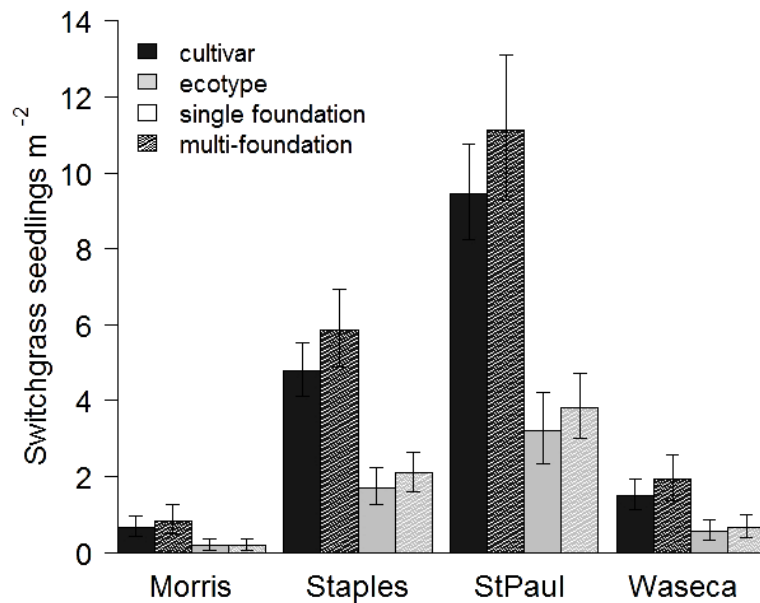


Fig. 2-11: Model-estimated effects (± 1 s.e.) of switchgrass breeding history and foundation-number on first-year switchgrass establishment in experimental prairies, analyzed jointly over four sites in Minnesota. Open bars: single-foundation. Hatched bars: multi-foundation.

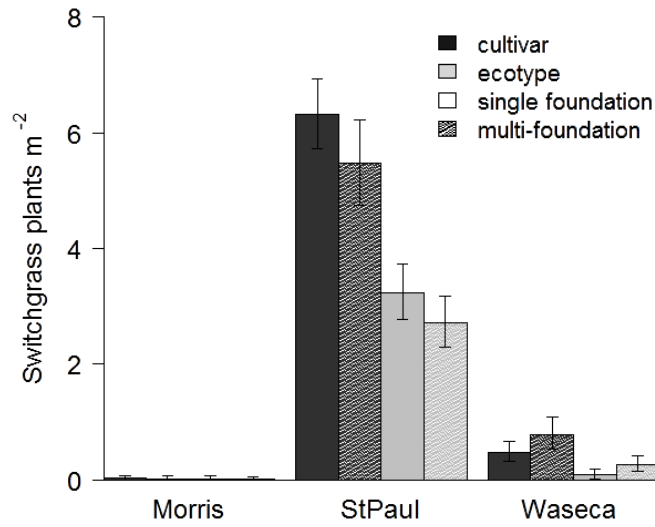


Fig. 2-12: Model-estimated effects (± 1 s.e.) of switchgrass breeding history, foundation-number, and site on third-year switchgrass stand density in experimental prairies, analyzed jointly over three sites in Minnesota. Open bars: single-foundation. Hatched bars: multi-foundation.

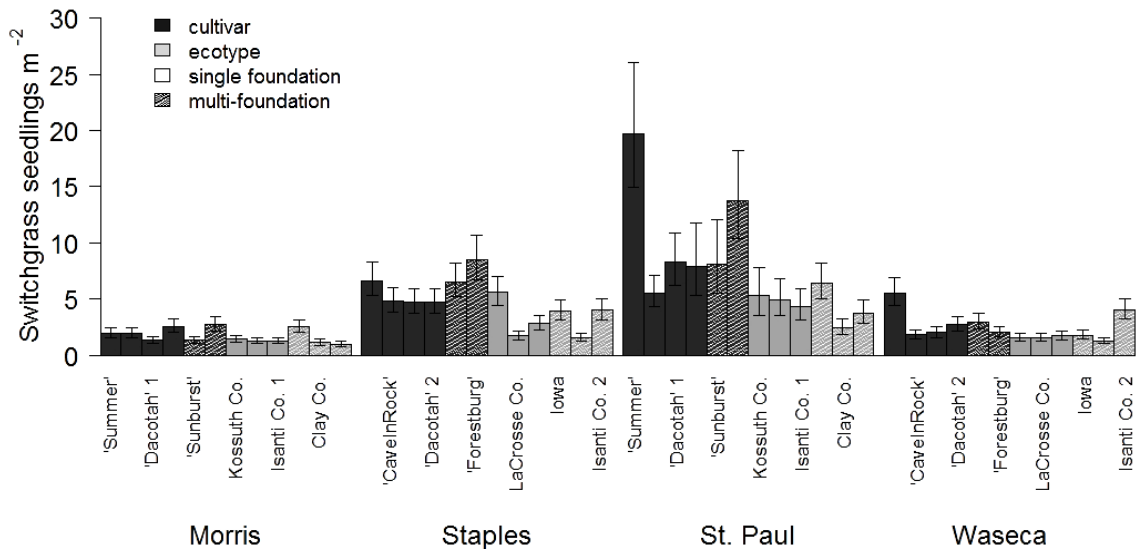


Fig. 2-13: Model-estimated effects (± 1 s.e.) of switchgrass strain on first-year switchgrass establishment in experimental prairies, analyzed jointly over four sites in Minnesota. Open bars: single-foundation. Hatched bars: multi-foundation. For clarity, strain names are shown for alternate bars.

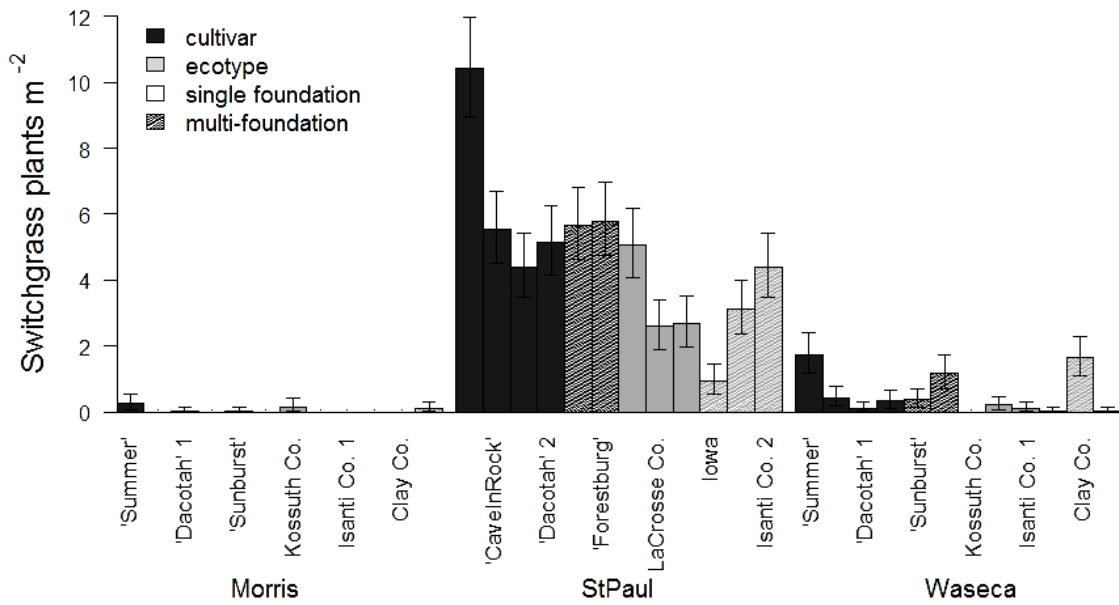


Fig. 2-14: Model-estimated effects (± 1 s.e.) of switchgrass strain on third-year establishment of switchgrass in experimental prairies, analyzed jointly over three sites in Minnesota. Open bars: single-foundation. Hatched bars: multi-foundation. For clarity, strain names are shown for alternate bars.

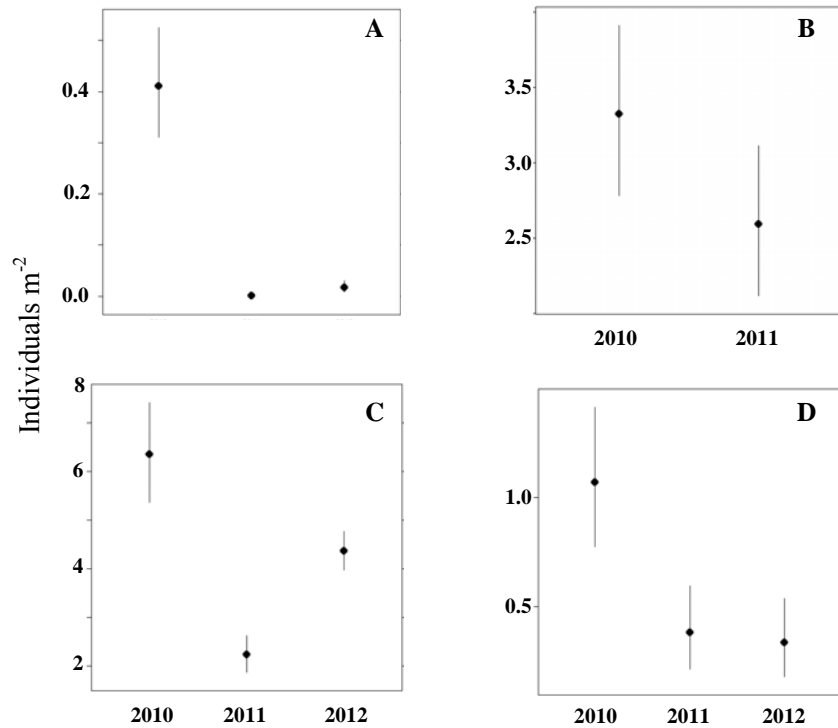


Fig. 2-15: Switchgrass stand densities (± 1 s.e.) after the first, second, and third growing seasons in experimental prairies in four sites in Minnesota: Morris (A), Staples (B), St. Paul (C), Waseca (D). Note differences in y-axis ranges.

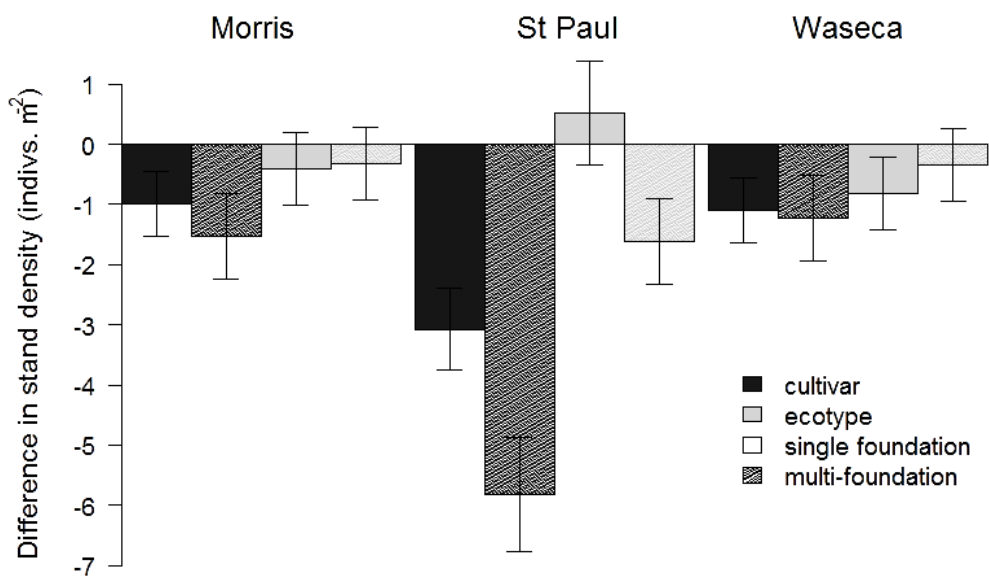


Fig. 2-16: Model-estimated effects (± 1 s.e.) of switchgrass breeding history, foundation-number and site on interannual differences in switchgrass stand density (3rd yr. - 1st yr.) in experimental prairies at three sites in Minnesota. Open bars: single-foundation. Hatched bars: multi-foundation.

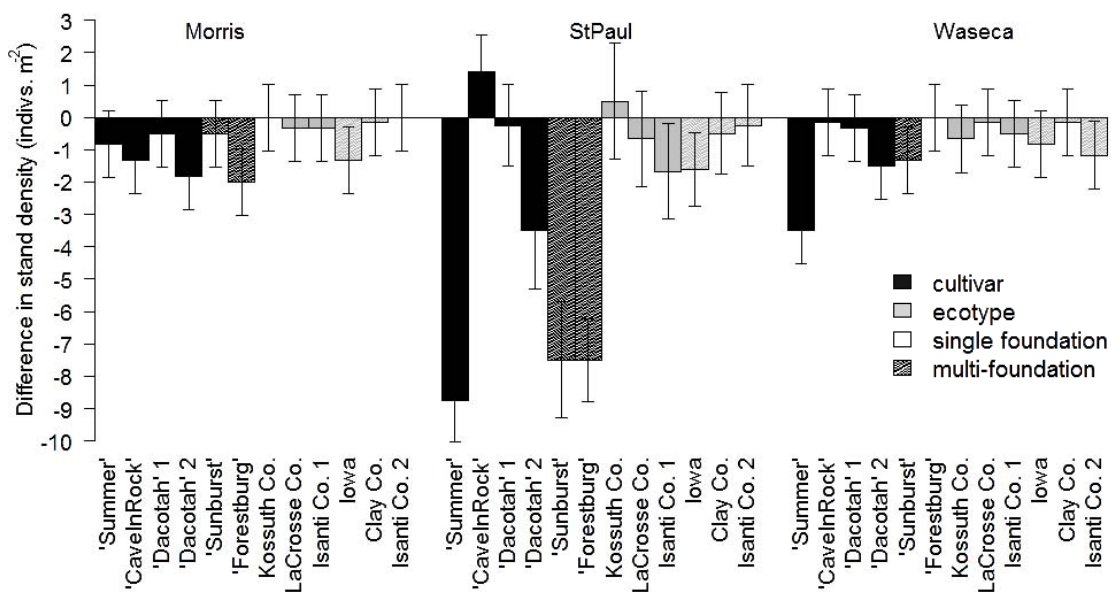


Fig. 2-17: Model-estimated effects (± 1 s.e.) of strain and site on interannual differences in switchgrass stand density (3rd yr. - 1st yr.) in experimental prairies at three sites in Minnesota. Open bars: single-foundation. Hatched bars: multi-foundation.

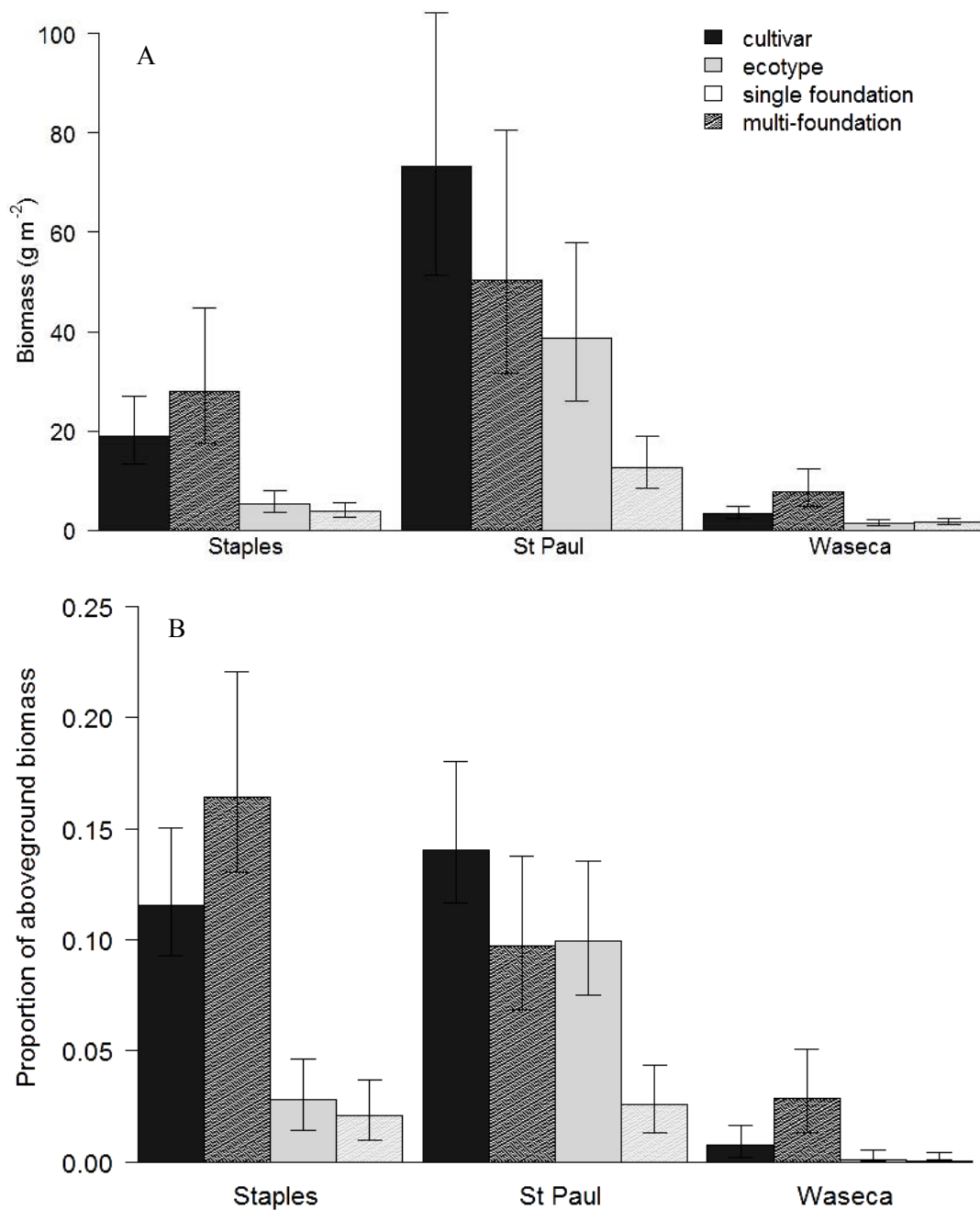


Fig. 2-18: Model-estimated effects (± 1 s.e.) of breeding history, foundation-number, and site on 3rd-year switchgrass aboveground biomass (A) and switchgrass proportion of community biomass (B) in three experimental prairies. Open bars: single-foundation. Hatched bars: multi-foundation.

Chapter 3:

Intraspecific differences in competitive response and effect in switchgrass (*Panicum virgatum* L.): Cultivars, ecotypes, and wild collections

Summary

The success of reconstructed grasslands depends on the establishment of target species despite weed competition. Community assembly is strongly affected by both inter- and intraspecific variation in competitiveness. One factor that may affect competitiveness but which has been little studied in this context is domestication intensity. In a greenhouse experiment, competitive response and effect were compared among three sources of switchgrass (*Panicum virgatum* L.) that range from strongly domesticated to non-domesticated. Using a full-factorial design, seed from switchgrass cultivated varieties (cultivars), commercially-produced but non-selected strains (ecotypes), and remnant prairie populations (wild collections) were grown against four associates: conspecifics (same strain); *Bromus inermis*, *Cirsium arvense*, and *Solanum ptycanthum*. Switchgrass competitive response was assessed as height, above- and belowground biomass, and relative interaction intensity. Competitive effect was assessed as associate height and above- and belowground biomass. Competitive response was lowest in wild collections. Ecotypes and cultivars performed similarly with two exceptions: cultivars exceeded the other groups in belowground biomass and ecotypes exceeded the other groups in above- to belowground and aboveground to total biomass ratios. Relative interaction intensity indicated that all switchgrass sources had weaker response to nightshade than to the other associates. Few differences in competitive effect on associates were detected between cultivars, ecotypes, and wild collections. However, belowground biomass of associates, particularly smooth brome, was smallest when grown against switchgrass cultivars. Domestication intensity affects intraspecific variation in switchgrass competitive ability. Taking domestication intensity and the identities of likely weed competitors into account during germplasm-sourcing decisions could improve the success of reconstructed grasslands.

Introduction

Grassland reconstructions (Kurtz, 2001) are increasing due to a growing recognition of the ecosystem services that they provide (e.g., Gascoigne *et al.*, 2011) and their potential importance as a source of sustainably-produced bioenergy feedstocks for the emerging bioeconomy (McCormick & Kautto, 2013). Because weed competition poses a significant challenge to reconstruction projects (Kurtz, 2001), factors that affect plant community assembly and structure are particularly salient for reconstructed grasslands. A substantial literature has demonstrated that community structure is strongly driven by interspecific variation in competitive outcomes (Goldberg & Barton, 1992; Allan *et al.*, 2011), particularly among dominant species (Gibson, 1988; Ervin & Wetzel, 2002). Such variation is affected by many factors, including herbivory, plant-soil relations, invasive species, and functional-guild similarity (e.g., Louault *et al.*, 2005; Jordan *et al.*, 2008; Mangla *et al.*, 2011; Larson *et al.*, 2013).

Community structure is also heavily influenced by intraspecific differences in competitiveness. Despite long-standing recognition that diversity at the species and genetic levels are profoundly connected (e.g., Antonovics, 1976, 1992; Aarssen, 1983; Amarasekare, 2000), the role of intraspecific variation has been largely overlooked until recently (Bolnick *et al.*, 2011; Violle *et al.*, 2012). Within grassland species, factors affecting variation in competition-relevant traits include mycorrhizal associations, resource availability, ecophysiology, and provenance (e.g., Hartnett *et al.*, 1993; Casper & Castelli, 2007; Lambert *et al.*, 2011; Gibson *et al.*, 2013). However, few studies have investigated differences in competitiveness within the context of domestication intensity, which is salient to germplasm-sourcing for grassland reconstructions.

Plant materials used in grassland reconstructions span a continuum from cultivated varieties (cultivars) developed through intense artificial selection to wild-harvested natural populations (wild collections); between these extremes lie strains that originated from natural populations (ecotypes, *sensu* Turesson, 1922) but were subsequently produced in increase fields where non-deliberate selective pressures were likely exerted (Aubry *et al.*, 2005). Cultivars, which are commonly selected for vigor (Moser & Vogel, 1995), are often grown in agronomic settings. In contrast, wild collections may produce poorly-performing seedlings as a result of environmental conditions that reduce pollination and maternal provisioning (Vogel, 2002). To the extent that differences in domestication intensity may influence competitive performance, germplasm choice will affect stand establishment, community assembly, and ultimately reconstruction outcomes. Low competitive ability may reduce yields of particular species in biofuel grasslands (Parrish & Fike, 2005) and facilitate colonization by invasive species (Lesica

& Allendorf, 1999; Zavaleta & Hulvey, 2004). However, strong competitive ability can depress community biodiversity (Baer *et al.*, 2005) and alter ecosystem function (Martin & Wilsey, 2012). If domestication intensity strongly affects competitive ability, then that characteristic should be considered in germplasm-sourcing decisions for grassland reconstructions.

Despite the possible importance of domestication intensity to intraspecific competitiveness in grasslands, few studies have examined this dynamic and the evidence is mixed. In a field-based comparison of a *Pseudoroegneria spicata* (*Poaceae*, C3) cultivar and wild collections, Lesica and Atthowe (2007) found that the cultivar was consistently larger, more fecund, and more suppressive of an invasive competitor, *Centaurea maculosa*. In glasshouse experiments, Gustafson *et al.* (2004a) found that one but not both cultivars of *Andropogon gerardii* (*Poaceae*, C4) were significantly larger than wild collections regardless of competitor density or identity (con- or heterospecifics). In a matched field experiment, however, shoot biomass did not differ among *A. gerardii* sources. Schröder and Prasse (2013) found that cultivars of *Plantago lanceolata* (*Plantaginaceae*) and *Lotus corniculatus* (*Fabaceae*) produced greater vegetative and reproductive biomass than wild collections in the glasshouse but the sources' relative performances varied among years in the field. In a glasshouse experiment, Walker *et al.* (2014) found that cultivars of three perennial grassland forbs had a stronger competitive response to a dominant grass (*Festuca rubra* ssp. *commutata*) than did commercial ecotypes; however, *F. rubra* cultivars had a weaker competitive effect on the forbs than did *F. rubra* ecotypes.

In this experiment, the effect of domestication intensity on differences in competitive ability among cultivar, ecotype, and wild strains of switchgrass (*Panicum virgatum* L.) was investigated. This North American, C4 grass species (*Poaceae*) is expected to be widely cultivated as a biomass and biofuel feedstock and is commonly used in grassland reconstructions. Although switchgrass sources have been compared with respect to effects on community composition (Wilsey, 2010), neutral genetic diversity (Casler *et al.* 2007a; Zalapa *et al.*, 2011; Zhang *et al.*, 2011; Mutegi *et al.*, 2014), and a host of agronomic traits (Parrish & Fike, 2005), direct assessments of competitive differences among switchgrass cultivars, ecotypes, and wild collections are lacking.

Intraspecific competitive ability was specifically assessed as switchgrass competitive effect, or its ability to suppress associates, and as switchgrass competitive response, its capacity for avoiding suppression by associates (Goldberg & Landa, 1991). To further elucidate observed patterns in competitive response, relative interaction intensity (RII, Armas *et al.*, 2004) was used to compare switchgrass sources in terms of the degree of suppression exerted by associates.

Because switchgrass is vulnerable to competition during emergence and establishment (Parrish & Fike, 2005) and because competition from establishing weeds can be intense, if transient, in reconstructed grasslands (Kurtz, 2001; Vogel, 2002), competitive effect and response were evaluated for juvenile switchgrass. A glasshouse experiment was used to address the following questions: (1) to what extent does response to conspecifics and common weedy associates vary among cultivar, ecotype, and wild sources of switchgrass? and (2) to what extent do these three switchgrass sources differ in their effects on those associates?

Methods

Switchgrass populations

Four of the populations used in this experiment - 'Summer' and 'Dacotah' and Kossuth County and Isanti County (1) ecotypes - are described in Table 1-2. The other two populations were collected under permit (2011-37R) during September and October, 2011 from the Felton-Shrike and Sandpiper Scientific and Natural Areas, Minnesota. Wild-collected seeds were allowed to after-ripen on the stem at room temperature (21°C) for two weeks, then were cleaned, packed with silica dessicant, and kept in cold storage (4°C, 50% humidity). All populations were stratified following Association of Official Seed Analysts guidelines (Meyer & Wiersema, 2009). To estimate seeding rates, germination tests were conducted on three lots of 50 stratified seeds per population, which were placed on moistened blotter paper in Parafilm[®]-sealed Petri dishes and incubated at room temperature under 8h:16h light:dark conditions. Germinated seeds (radicle visible to the naked eye) were counted and removed every seven days for three weeks. Mean percent germination was 48% and 65% for 'Summer' and 'Dacotah', respectively; 39% and 67% for the Kossuth and Isanti County ecotypes, respectively; and 8% and 4%, respectively, for the Felton-Shrike and Sandpiper wild collections.

Associate species

Smooth brome (*Bromus inermis* Leyss.) is a perennial C3 (cool-season) grass native to Eurasia (Salesman & Thompson, 2011) that was deliberately introduced to the US in the 1880s as a forage crop (Newell & Anderson, 1962). It is considered weedy or invasive in the upper Midwestern U.S. (Stubbendieck *et al.*, 1994) where it has colonized tall- and mixed-grass prairies, particularly in disturbed or nutrient-enriched areas (Larson *et al.*, 2001). At local scales, it has replaced switchgrass and other native species (Vinton & Goergen, 2006).

Canada thistle (*Cirsium arvense* (L.) Scop.) is an imperfectly-dioecious (Donald, 1994), insect-pollinated perennial forb native to Eurasia. Introduced to the American colonies as a crop-seed contaminant, it is listed as noxious in all of the Canadian provinces and in much of the US (Moore, 1975; Mitich, 1988). It is a problematic and ubiquitous invader of restored tall- and mixed-grass prairies (Almquist & Lym, 2010; Larson *et al.*, 2013).

Eastern black nightshade (*Solanum ptychanthum* Dunal) is an annual forb and a common, significant agricultural weed (Ogg *et al.*, 1981). Native to North America, eastern black nightshade occurs throughout most of the conterminous US and southern Canada (USDA NRCS 2015). It can germinate and fruit within six weeks but persist and reproduce for several additional months (Ogg *et al.*, 1981). Some Midwestern populations of eastern black nightshade have evolved resistance to imidazolinone herbicides (Volenberg *et al.*, 2007); this family of acetolactate synthase-inhibitors can be effective at suppressing weed competition in restorations (Masters *et al.*, 1996; Bahm & Barnes, 2011). Due to its plasticity (Hermanutz & Weaver, 1996), ubiquity, and capacity for evolving resistance, eastern black nightshade is likely to be common in establishing grasslands.

Associate-species seeds for the experiment were obtained as follows: smooth brome (variety not specified) was purchased from Albert Lea Seed (Albert Lea, MN, seed lot 868); Canada thistle was wild-harvested in Olmsted County, MN and transported under permit (1-2010-MDA4) by Dana Olofson and Sheri Huerd; eastern black nightshade was originally purchased from Valley Seed Service (Fresno, CA, lot number not available) and supplied by Sheri Huerd and Nicholas Jordan, University of Minnesota Department of Agronomy and Plant Genetics. Germination tests were as described above, except six lots per species were tested, incubations were in the dark, and the tests ran for 28 days. Mean germination percentages were 45%, 10%, and 60% for the brome, thistle, and nightshade, respectively.

Experimental design

This competition experiment had a simple-pairwise (Gibson 2015), full-factorial, randomized-complete block design. In every pot, one switchgrass individual (target) was grown with one individual of either an associate species or an individual from the same switchgrass strain (associate). Five replicates of each target-associate combination were randomly assigned to positions in each of five blocks, for 600 total pots (5 replicates x 6 switchgrass strains x 4 associate species x 5 blocks = 600). Associate-species monocultures (i.e., a diallel design, Gibson 2015) were not utilized because space constraints would have required less replication.

D40 cone-tainers® (Stuewe & Sons) were filled with a 1:1 ratio of commercial potting mix (Sunshine MVP®, Hummert International) and autoclaved field soil (silt loam, St. Paul, MN) and thoroughly watered. To increase the likelihood of successful establishment, target and associate seeds were sown at twice the density indicated by germination test results. Seeds were then covered with a 1 cm-thick layer of vermiculite and lightly watered. Seedlings were not present in 26 pots on the 21st day after sowing; these were reseeded on day 22 but not subsequently. Surplus seedlings were removed by clipping at soil level. All pots were lightly watered daily for the first four weeks; subsequently, all were watered thoroughly, every other day. To address chlorosis in the associate forb species, 2 g of a slow-release N-P-K fertilizer (Osmocote Plus® 14-14-14) was added to all pots during the fifth week. Nutrient addition was also anticipated to reduce the negative impacts of soil sterilization on plant nutrient status, as all species in this experiment form mycorrhizal associations (Klironomos, 2003; Parrish & Fike, 2005; Jordan & Huerd, 2008).

Data collection and analysis

At 16 weeks after seeding, the maximum height of each plant was measured and plants were harvested. Individuals from two random blocks were separated into aboveground and belowground fractions; the latter were rinsed thoroughly with filtered water and allowed to air-dry. Due to time constraints, only aboveground biomass was harvested from the remaining three blocks. All samples were then dried at 60°C for 72 hours. Samples weighing < 0.1 g were assigned a value of 0.05 g.

Target performance was measured as height; aboveground, belowground and total biomass; ratios of above- to belowground and aboveground to total biomass; and relative interaction intensity (RII, Armas *et al.*, 2004). This index can be expressed as $(B_w - B_o) / (B_w + B_o)$, where B_w and B_o are biomass values for a target plant grown respectively with, and without, a competitor. Values can range from -1 to 1 and indicate the intensity of competitive ($-1 \leq \text{RII} < 0$) or facilitative ($0 < \text{RII} \leq 1$) interactions. Separate RII values were calculated using aboveground, belowground, and total target biomass. To estimate B_o for each switchgrass source, the mean biomass value was calculated for target plants whose associate had not established; n for these means ranged from 11 to 43. Associate performance was measured as height, aboveground, belowground, and total biomass, and the ratio of above- to belowground biomass.

Univariate mixed-effects models (*lmer*) from the *lme4* package (Bates *et al.*, 2015) in *R* (v. 3.1.0, R Core Team 2013) were used to test for variation among switchgrass sources in

competitive effect, response, and interaction intensity. Switchgrass source and associate identity were fixed effects and block was modeled as a random effect. Residuals were visually assessed for normality and homoscedasticity. Responses were transformed when necessary to improve compliance with model assumptions: height was square-root transformed; biomass and biomass ratios were log-transformed; RII values were not transformed.

Results

As measured by switchgrass performance, competitive response was generally lowest in wild collections, similar for cultivars and ecotypes, and varied across associates. Switchgrass height ($F_{2, 438} = 31.8, p < 0.0001$), aboveground ($F_{2, 438} = 15.1, p < 0.0001$), and total biomass ($F_{2, 157} = 9.14, p = 0.00018$) differed among sources: wild collections had the lowest values of all three measures but there was no evidence of difference between cultivars and ecotypes (Fig. 3-1, Fig. 3-2). Belowground biomass also differed among sources ($F_{2, 157} = 8.26, p = 0.00039$), with cultivars exceeding both ecotypes and wild collections (Fig. 3-2). Sources also differed with respect to the ratios of above- to belowground ($F_{2, 157} = 12.7, p < 0.0001$) and aboveground to total ($F_{2, 157} = 12.8, p < 0.0001$) biomass. Ecotype ratios were greater than those of both cultivars and wild collections (Fig. 3-3).

Competitive response was strongly influenced by associate identity, which affected switchgrass height ($F_{3, 438} = 53.4, p < 0.0001$); aboveground ($F_{3, 438} = 52.2, p < 0.0001$), belowground ($F_{3, 157} = 41.7, p < 0.0001$), and total biomass ($F_{3, 157} = 32.3, p < 0.0001$); and ratios of aboveground:belowground ($F_{3, 157} = 9.71, p < 0.0001$) and aboveground:total biomass ($F_{3, 157} = 9.88, p < 0.0001$). All switchgrass sources were shortest, smallest, and allocated most to aboveground biomass when grown with nightshade (Fig. 3-2, Fig. 3-3). Across sources, target height significantly increased when grown against associates in this order: nightshade > thistle > control > brome (Fig 3-1). Significant differences were not detected for target biomass and biomass ratios among the thistle, control, and brome treatments; however, cultivar total biomass was approximately 30% greater when associated with brome than with the other species (Fig. 3-2).

Uniformly negative RII values confirmed that switchgrass response to associates was competitive rather than facilitative (Fig. 3-4). The strength of response to competition, as measured by RII values, did not differ detectably among switchgrass sources. However, RII values strongly differed among associate species, whether calculated with aboveground ($F_{3, 438} = 40.8, p < 0.0001$), belowground ($F_{3, 157} = 31.8, p < 0.0001$), or total ($F_{3, 157} = 25.0, p < 0.0001$)

switchgrass biomass. Consistent with the biomass results, competition was most severe when nightshade was the associate. Cultivars were least, and ecotypes were most, affected by competition with brome and cultivars were most impacted by nightshade (Fig. 3-4), although the source x associate interaction for RII was non-significant.

The competitive effect of switchgrass sources, as measured by associate height and biomass, varied significantly among performance measures. Switchgrass source did not affect associate height, aboveground biomass, aboveground:belowground or aboveground:total biomass ratios. However, associate belowground ($F_{2, 158} = 4.42, p = 0.014$) and total biomass ($F_{2, 158} = 4.62, p = 0.011$) values were lowest when the targets were cultivars; the pattern was particularly notable for brome associates (Fig. 3-5). Associate biomass was highly variable when grown with either ecotypes or wild collections and did not differ significantly between those two sources. However, the mean biomass of heterospecific associates was generally higher for wild collections than ecotypes (Fig. 3-5).

Discussion

Domestication history in switchgrass contributes to intraspecific variation in competitive response and effect at the seedling stage. When grown in association with heterospecific competitors that are common to reconstructed grasslands, cultivars consistently outperformed wild collections but demonstrated similar competitive responses to switchgrass ecotypes, with the exception of belowground biomass. Cultivars exerted stronger competitive effects, however, particularly on smooth brome. As reported by other glasshouse studies, the relationship between competitive ability and domestication history is contingent on associate identity. Wilsey (2010) found that germination rates of cultivars exceeded those of wild collections in switchgrass, *Bouteloua curtipendula*, *Sorghastrum nutans*, and *Schizachyrium scoparium*; however, the pattern was reversed for *A. gerardii*. Gustafson *et al.* (2004a) reported that one but not both *A. gerardii* cultivars exceeded wild collections in height and biomass. Finally, while forb cultivars were less suppressed by competition than ecotypes, the converse was true for a grass species (Walker *et al.*, 2014).

It is unlikely that similarities between cultivars and ecotypes in height and biomass are due to cultivar under-performance or maladaptation to experimental conditions. Some switchgrass cultivars have been selected for traits such as foliage color (Thetford, 2009); however, ‘Dacotah’ (USDA NRCS 1990) was selected for vigor. ‘Summer’, which was selected for leafiness (Alderson & Sharp, 1995) is known to be a high-yielding strain (Delaquis *et al.*,

2014). Switchgrass generally is adapted to a wide range of soil textures and nutrient regimes (Parrish & Fike, 2005) and the growing medium used in this experiment was well within these limits. Selected cultivars are intended for use in specified environments (Casler & van Santen, 2010), which for ‘Dacotah’ and ‘Summer’ include mesic loams in the upper Missouri and Minnesota River basins that were mimicked by our experimental light, water, and soil regimes.

Unintentional selection can occur during ecotype production (McKay *et al.*, 2005) and evolution in various traits has occurred in seed-production fields over short time-spans (Knapp & Rice, 1994). Such selection could have shifted trait means in ecotypes towards those of cultivars, perhaps explaining the similarity between cultivar and ecotype performance. Harvest and seed-cleaning methods could inadvertently select for increased seed mass, which is strongly influenced by maternal environment (Bischoff *et al.*, 2006) and is positively related to germination and seedling establishment in switchgrass (Aiken & Springer, 1995). To the extent that maternal vigor is genetically rather than environmentally influenced, supplementing an increase field with its own progeny could impose selection for more strongly-competitive plants.

These findings indicate that adaptive differentiation may exist among switchgrass sources. Ecotypes exceeded the other sources in aboveground allocation of biomass, especially when grown with nightshade. Weed competition is common in commercial seed-production fields (Dunne & Dunne, 2002) and associated light-limitation could exert selective pressure for greater aboveground growth. In contrast, cultivars both suppressed brome root biomass and produced more belowground biomass, particularly when associated with brome. Until very recently, switchgrass cultivars have been developed primarily as forage crops (Parrish & Fike, 2005), which implies competition from perennial C3 grasses and selection for increased belowground biomass that could enhance resource capture and vernal resprouting.

All switchgrass sources allocated proportionately more biomass to aboveground tissues when associated with nightshade than with the other species, demonstrating that competitive responses in switchgrass are plastic. If so, and if the capacity for plastic response is partially genetically determined, plasticity may be a useful target for germplasm development. Weed competition is a primary obstacle to successful grassland reconstruction and plasticity in competitive response, as well as overall vigor, could contribute to successful stand establishment.

The duration of this study was limited to 16 weeks to minimize the extent of root-binding in the plants. This time constraint notably affects the interpretation of two results. First, the differences between cultivars and ecotypes in height and biomass - the mean values of which were greater in cultivars - may have amplified or diminished during a longer experiment. This

could have resulted in either significantly greater cultivar biomass, as was observed in some experimental prairie plots (Chap. 2), or in similar values for cultivar and ecotype biomass, as observed in sown switchgrass monocultures (Chap. 1). Second, although germination and performance were lower in wild collections than in either cultivars or ecotypes, the three sources did not differ with regards to RII. Being smaller, the wild collections may not have been in strong competition with associates by the conclusion of the experiment and a longer study might have revealed among-source differences in RII.

Maternal effects, which confound seedling performance with maternal genotype and environment (Roach & Wulff, 1987), were not addressed within our experimental design and may have influenced outcomes. The cultivar and ecotype seeds used in this study were produced in commercial increase fields, whereas the wild collections were obtained from relatively small and fragmented natural populations. The comparatively weak performance of seedlings from wild collections may thus reflect low values for heritable traits, unfavorable environmental conditions experienced by maternal plants, or both. Due to time constraints, maternal effects could not be reducing through rearing a parental generation in a common environment and using the resulting progeny in the experiment.

The design of this experiment introduced two factors that likely affected outcomes and inference. First, seed dormancy is a well-known source of differential performance between cultivars and wild collections (*e.g.*, Casler *et al.*, 2007a) but was not addressed in this study. Pots were deliberately over-seeded to maximize replication. Second, this experiment was conducted under a single set of controlled, glasshouse conditions. Cultivars of various species have exhibited differential performance in glasshouse versus field and in cultivated versus non-cultivated conditions (Anderson *et al.*, 2006a). Additional research is needed to confirm whether the findings presented here are replicable under environmentally realistic conditions.

Conclusions

Domestication intensity strongly affects switchgrass competitiveness. Juvenile competitive response in switchgrass ecotypes and cultivars was similar; however, both had stronger responses than wild collections. Further, some competitive effects exerted by cultivars are stronger than those shown by commercial ecotypes or wild collections. Associate interactions were uniformly competitive rather than facilitative and all sources of switchgrass were more suppressed by an annual forb than by perennial species. Switchgrass may establish poorly in sites

with high densities of weeds, especially annuals, underscoring the need for adequate site preparation and weed control in reconstructed grasslands.

Cultivars are more effective than ecotypes at suppressing cool-season grasses but ecotypes had stronger competitive response to eastern black nightshade. Insofar as cultivars have been selected as forage grasses and ecotypes have been agronomically produced, switchgrass populations may be differentially adapted to relatively recent selective pressures. Therefore, taking switchgrass domestication intensity and expected competitor identities into account during germplasm-sourcing decisions could improve the success of reconstructed grasslands. However, only two strains of each source were examined; additional competition experiments are needed to test the generality of these results. These findings should not be extended to lowland cultivars, which are generally larger and more productive than the upland strains investigated in this study.

Wild-collected switchgrass populations exhibited the weakest competitive response and effect, possibly because of poor seed provisioning, low-quality maternal environment, or inbreeding depression. Because remnant populations represent reservoirs of genetic diversity that may benefit future switchgrass breeding efforts, conditions at these populations should be assessed and managed to improve population stability, fitness, and genetic diversity.

Figures

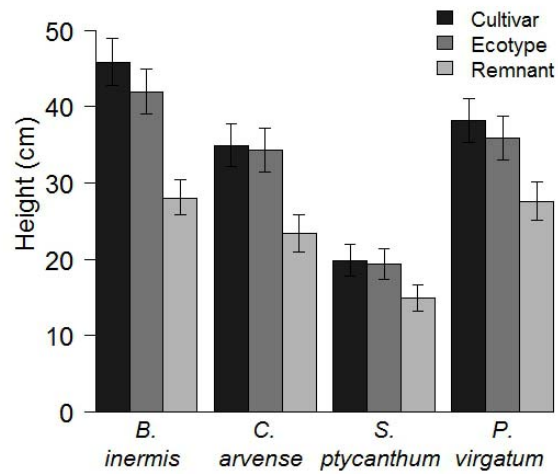


Fig. 3-1: Back-transformed (square-root) model-predicted mean height (\pm SE) of switchgrass cultivars, ecotypes, and wild collections grown in competition with 4 associate species.

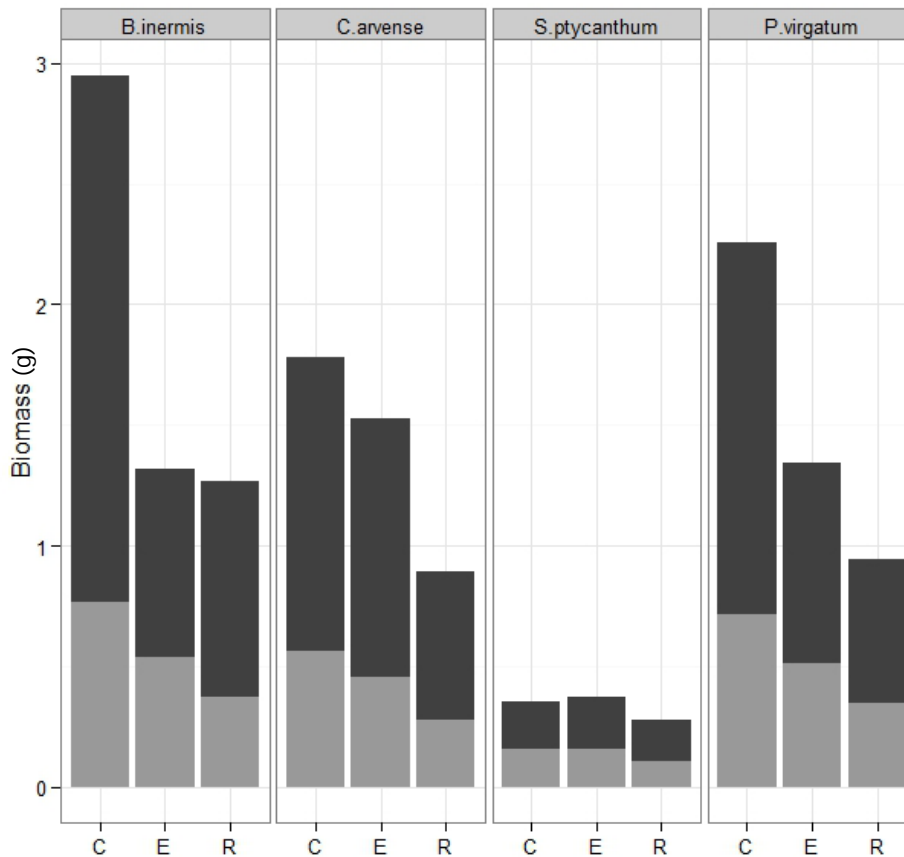


Fig. 3-2: Back-transformed (log) model-predicted mean aboveground (light gray), belowground (dark gray), and total (total bar height) biomass of switchgrass cultivars (C), ecotypes (E), and wild collections (R), grown in competition with 4 associate species. $N = 2$ for each switchgrass source. To improve figure clarity, error bars are not shown.

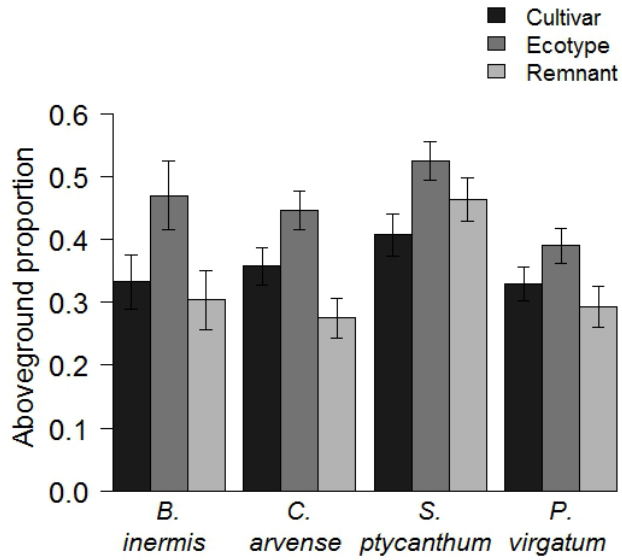


Fig. 3-3: Model-predicted mean (\pm SE) proportion of aboveground to total switchgrass biomass for cultivars, ecotypes, and wild collections grown in competition with 4 associate species. $N = 2$ for each switchgrass source.

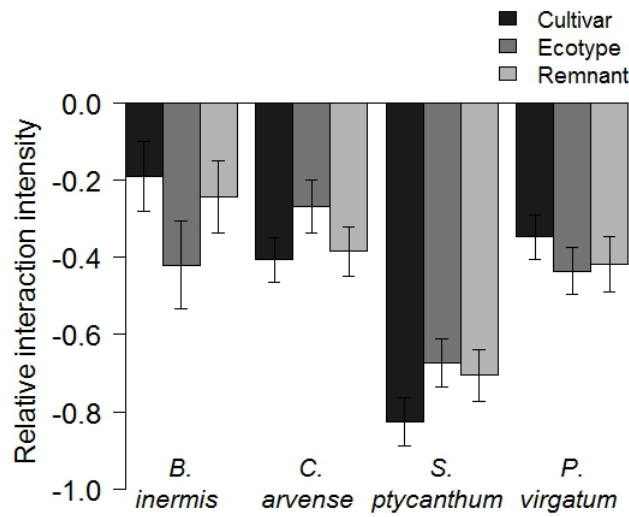


Fig. 3-4: Model-predicted mean (\pm SE) relative interaction intensity for switchgrass cultivars, ecotypes, and wild collections grown in competition with 4 associate species. $N = 2$ for each switchgrass source. See text for details of RII calculations.

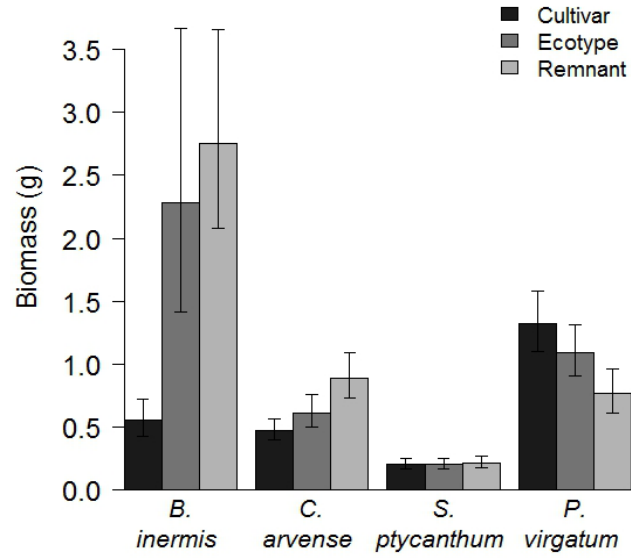


Fig. 3-5: Back-transformed (log) model-predicted mean belowground biomass of 4 associate species grown in competition with switchgrass cultivars, ecotypes, and wild collections. N = 2 for each switchgrass source.

Dissertation Conclusions

I found little evidence that switchgrass is likely either to become overly dominant in reconstructed grasslands or invasive in adjacent areas; however, taking both switchgrass source and the identity of anticipated competitors into account may contribute to successful establishment in reconstructed grasslands. I did not find that multi-foundation strains performed better across sites than their single-foundation counterparts, perhaps because of insufficient experimental duration, homogeneity among sites, or similar levels of genetic diversity between multi- and single-foundation strains.

Rather than focusing on invasiveness or stand failure, assessments of risk related to switchgrass translocation should investigate four key questions: (1) what is the spatial scale of local adaptation in switchgrass for fitness-related traits? (2) what is the range of quantitative genetic variance for fitness-related traits in wild switchgrass populations? (3) what management strategies will most effectively enhance and support the genetic diversity and long-term persistence of wild switchgrass populations? (4) how can negative impacts of gene flow between translocated and wild switchgrass populations be adequately mitigated? If we fail to adequately address these questions prior to large-scale switchgrass translocations, we risk eroding the genetic diversity that could confer switchgrass resilience to pests, pathogens, and rapid environmental change.

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